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STRUCTURE AND FUNCTION OF THE SENSE ORGANS ON THE LABIUM, FASCICULAR STYLETS, CIBARIUM AND TARSI OF MOSQUITOES

by

© ROBERT MAUNG KYAW WIN LEE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Structure and Function of the Sense Organs on the Labium, Fascicular Stylets, Cibarium and Tarsi of Mosquitoes submitted by Robert Maung Kyaw Win Lee in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Structure of the sense organs on the labella and labium of Aedes aegypti was studied with light (LM), scanning (SEM) and transmission (TEM) electron microscopes. The distribution of these sense organs are similar in both sexes. Both mechano- and chemoreceptive hairs are found on the aboral surfaces of the labellar lobes. Apical hairs invaginated inside the labellar lobes, and the oral papillae are probably chemoreceptive. A chordotonal organ with two nerve cells is found in each labellar lobe. The labial hairs resemble mechanoreceptors. Ligular hairs are not sensory.

The labra of both sexes of 40 mosquito species belonging to 15 genera were studied using SEM, and 10 species using LM. It seems the presence of apical and subapical labral sensilla is related to the blood sucking habits of mosquitoes. The openings of these sensilla are located near the tip and they are often occluded by a substance probably secreted by the sensilla. Deinocerites pseudes and Culex species are different from other species in having the campaniform sensilla positioned inside the food canal. Cuticular microsculpture on the dorsal wall of the labrum is absent from some species and the shape differs between species.

Mandibles of 10 species of female mosquitoes belonging to six genera were examined using SEM. Teeth are found only in Armigeres durhami and Anopheles species.

Cuticular hair-like projections are found at the tip of the hypopharynx in 26 species of female mosquitoes representing 11 genera.

The laciniae of 31 species of female mosquitoes belonging to 14 genera were examined using SEM. The number of lateral teeth, and the presence or absence of mesial teeth are discussed in relation to the host(s) of the mosquitoes.

The position and type of cibarial sense organs in 37 species of mosquitoes representing 10 genera were studied using LM, and the cibaria of five species were studied using SEM. Differences are found between species, and even between sexes of the same species. Taxonomic importance of the cibarial armature is discussed.

Preliminary study of the tarsal hairs in A. aegypti showed that the double-lumina hairs are probably chemoreceptive.

The possible function of the sense organs described in this study is discussed in relation to the feeding behaviour of the mosquitoes.

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I. INTRODUCTION

Because of the medical and economic importance of mosquitoes, the study of the sense organs and feeding behaviour of mosquitoes has attracted the attention of many researchers.

Some mosquitoes are attracted at a long distance by host odours, at middle range by CO_2, and at close range by warmth, humidity and visual stimuli (Gillies and Wilkes, 1969). Movement of the host has a small, but consistent positive attraction (Wood and Wright, 1968). Antennal receptors of mosquitoes are reported to respond to humidity (Roth, 1951; Daykin et al., 1965; Kellogg, 1970), to temperature (Ismail, 1962; Daykin et al., 1965; Davis and Sokolove, 1975) and to repellents (Steward and Atwood, 1963; Daykin et al., 1965; Lacher, 1967; Davis and Robert, 1972). CO_2 receptors are located on the maxillary palps (Kellogg, 1970).

Discrimination after the mosquito has landed on a host may be a function of the tarsal hairs. Tarsal chemosensory hairs have already been reported in different species of mosquitoes (Frings and Hamrum, 1950; Wallis, 1954; Feir et al., 1961; Slifer, 1961; Owen, 1963, 1967, 1971). In probing to find a suitable spot for feeding, the mosquito uses the two labellar lobes located at the tip of the long, gutter-like labium (Nuttall and Shipley, 1901; Schiemenz, 1957; Clements, 1963). A short ligula is situated between the two labellar lobes. According to Snodgrass (1957), the mosquito labium is the prementum of a generalized insect.

A fascicle composed of six stylets (one labral, two mandibular, one hypopharyngeal and two maxillary) is contained inside the labial gutter. Distally, the fascicle projects out between the two labellar lobes dorsal to the ligula. During piercing and sucking, the labium with the labellar lobes remain outside the host tissue, with only the fascicle penetrating the host tissue; the labrum forms the food canal. A muscular cibarial pump under the clypeus is attached to the proximal end of the labral food canal.

The structure of the labellar sense organs in mosquitoes has been studied using light microscopy (LM) (Vogel, 1921; Frings and Hamrum, 1950; Feir et al., 1961; Zwonitzer, 1962; Owen, 1963, 1971), scanning electron microscopy (SEM) (Pearson, 1970), and transmission electron microscopy (TEM) (Chaika and Elizarov, 1971; Larsen and Owen, 1971; Owen et al., 1974). Behavioural (Frings and Hamrum, 1950; Hosoi, 1954; Feir et al., 1961; Owen, 1963, 1967, 1971; Salama, 1966; Larsen and Owen, 1971;Owen et al.,1974) and electrophysiological studies (Zwonitzer 1969; Pearson, 1970; Owen et al., 1974) have been made to elucidate the function of the labellar hairs. However, functional studies of the labellar hairs were conducted mostly on one type of hair, mainly because all labellar hairs were considered structurally similar. A thorough knowledge of the distribution and fine structure of the labellar sense organs is still lacking.

Of the six fascicular stylets, only the labrum bears sense organs (Vogel, 1921; Schiemenz, 1957; Lee, 1974). Description of the labral sense organs was incomplete, as most authors failed to notice all the labral sense organs (see von Gernet and Buerger, 1966, and Lee, 1974 for review).

Several types of sense organs are present inside the cibarial pump (Day, 1954; Lee, 1974), and the importance of these sense organs in food discrimination has been emphasized by many workers (Day, 1954; Hosoi, 1959; Owen, 1963, 1965; Salama, 1966; Pearson, 1970). Fine structure of these sense organs remains undescribed, because of the difficulty in dissecting the cibarium.

As the use of insecticides to control mosquitoes has become more and more costly both economically and ecologically, there is a need for alternative measures against mosquito bites, and the development of longer lasting systemic repellents "has been the dream of many scientists for years" (Weidhaas, 1972). Compounds have been screened for potential systemic repellents, but the search was unsuccessful (Weidhaas, 1972). This may be partly due to the meagre knowledge we have on the sense organs involved in the feeding behaviour of the mosquitoes. This present study was undertaken to investigate the structure of the sense organs involved in mosquito feeding, thereby laying a foundation for future electrophysiological studies to understand the functions of these sense organs. This may lead to a more rational testing of chemicals for mosquito repellents.

In this study, the structure of the sense organs on the labium and the tarsi of both sexes of Aedes aegypti, of the labral and cibarial sense organs in 15 genera of mosquitoes, and of the fascicular stylets in different species of mosquitoes were studied using LM, SEM and TEM. These observations are integrated into the present body of knowledge on the sense organs on the mouthparts of mosquitoes.

II. MATERIALS AND METHODS

A culture of Aedes aegypti was maintained in the insectary at 27°C and 65% R.H. with eggs kindly donated by Dr. A. S. West (Department of Biology, Queen's University, Kingston, Ontario, Canada). Live Culiseta inornata were obtained from a culture maintained by my colleague Mr. J. Hudson. Other mosquito species were either collected locally, or obtained through generous donations of various people (see Appendices A and B for species and source list). Methods of preparation for LM, SEM and TEM were the same as described by Lee (1974). Burgess and Rempel's (1966) method for vital methylene blue staining was used. The following method was used to study the cibarial sense organs.

The specimens were fixed in 5% formalin. The labrum was unsheathed from the labium using the method of MacGregor (1930). A tungsten wire needle was then inserted between the clypeus and the cibarium, and the elevator muscles of the cibarium detached from the clypeus. By pulling the labrum horizontally away from the head, the cibarium normally comes out attached to the proximal end of the labrum. It was then dehydrated through a series of ethanol. Muscles still attached to the cibarium were removed using fine forceps when the specimens were in 98% alcohol. For Toxorhynchites species where the attachment of the muscles to the cibarium is firm, the cibarium with labrum attached to it was boiled in 10% KOH for five to ten minutes, then washed in several changes of distilled water, followed by dehydration in ethanol.

After dehydration, the specimens were cleared in xylene. For LM, the specimens were mounted in DPX. For SEM, the specimens were air-dried. Sense organs on the dorsal wall of the cibarium were exposed using the following procedure. The dorsal side of the cibarium was attached to a specimen stub with a drop of Silver Dag (Ted Pella Co.). An electrolytically etched fine tungsten wire was inserted between the hypopharynx and the labrum into the cibarial lumen, and the upper wall of the cibarium was removed gently by raising the tungsten needle, exposing the inner surface of the cibarium. The same procedure was used to study the sense organs on the ventral cibarial wall, except the ventral wall of the cibarium was now attached to the stub. The specimens were then coated with 150 Å of carbon and gold, and observed with a Cambridge Stereoscan S4 scanning electron microscope.

III. RESULTS AND DISCUSSION

1. Labium

The following description applies to both sexes of Aedes aegypti, as the distribution and the structure of the labellar and labial sense organs are similar in both sexes.

1.1. Labella

The two labellar lobes at the tip of the labium together form a pear-shaped structure (Figs. 1, 3). Each labellum is two segmented. The two segments abut obliquely to each other on the dorsal surface (Fig. 1), and horizontally on the ventral surface (Fig. 3). A ligula covered with hairs projects out between the two labellar lobes (Fig. 5), and contains the tip of the fascicle on its trough-shaped dorsal surface. As the concave inner surfaces of the labella are facing the labral food canal, I will refer to the inner surface of the labellum as the oral surface, and the outer convex surface of the labellum as the aboral surface. A similar system is used for blowfly labella (Dethier, 1955).

The labellar lobes of mosquitoes were considered by many workers as important in serving as a guide for the fascicle during piercing and sucking, but Robinson (1939) found that mosquitoes with their labella removed were still able to feed on a host quite normally. Therefore he suggested that the labella serve to allow instant return of the stylets to the labial gutter after withdrawal, and that the

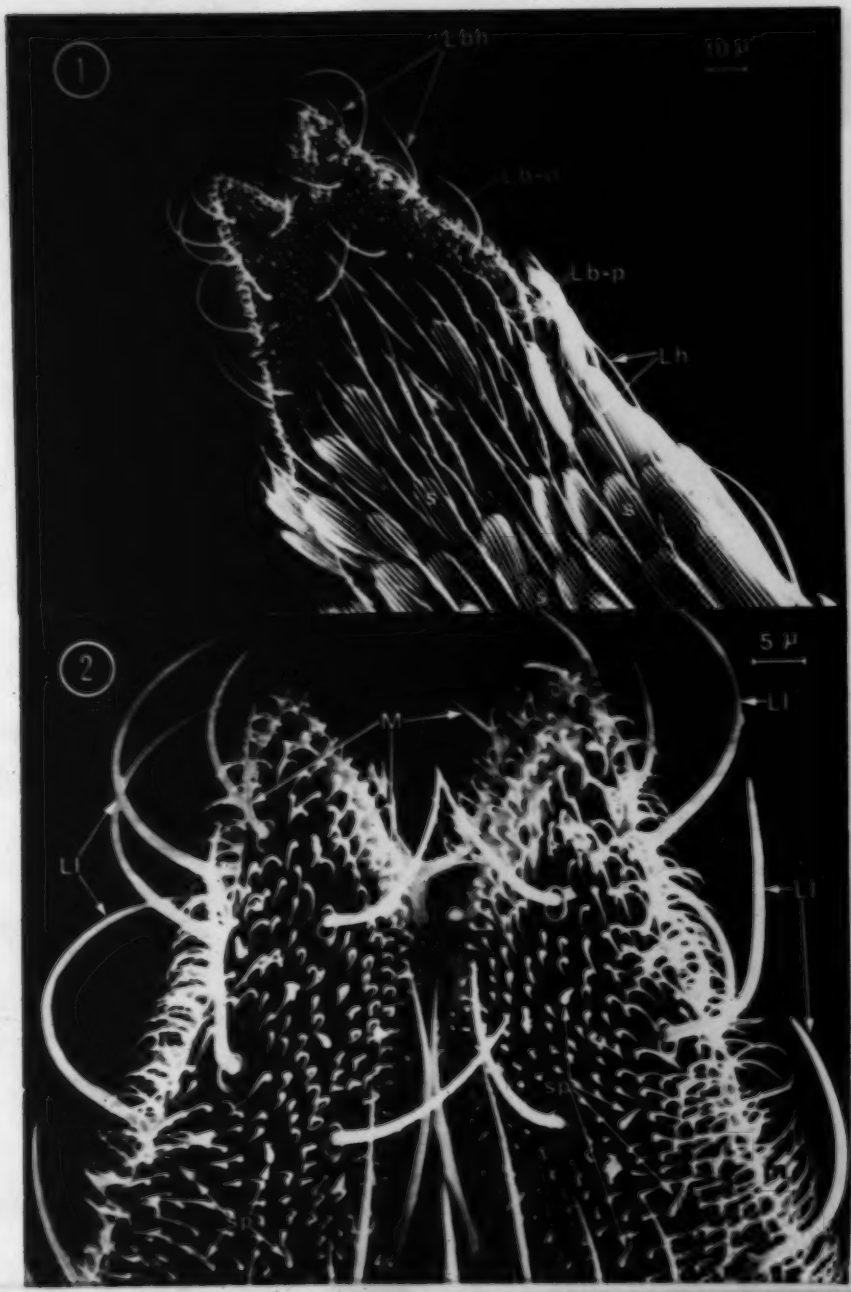


Fig. 1. Dorsal aspect of female Aedes aegypti, showing labellar (lhb) and labial (Lh) hairs. Each labellum is composed of a distal (Lb-d) and proximal (Lb-p) segments. Scales (s) are found on the proximal labellar segment.

Fig. 2. Same at higher magnification, showing different types of labellar hairs. Ll, long labellar hairs; M, medium-sized hairs; m, microtrichia; sp, short papillae. The short papillae are also socketed at the base.

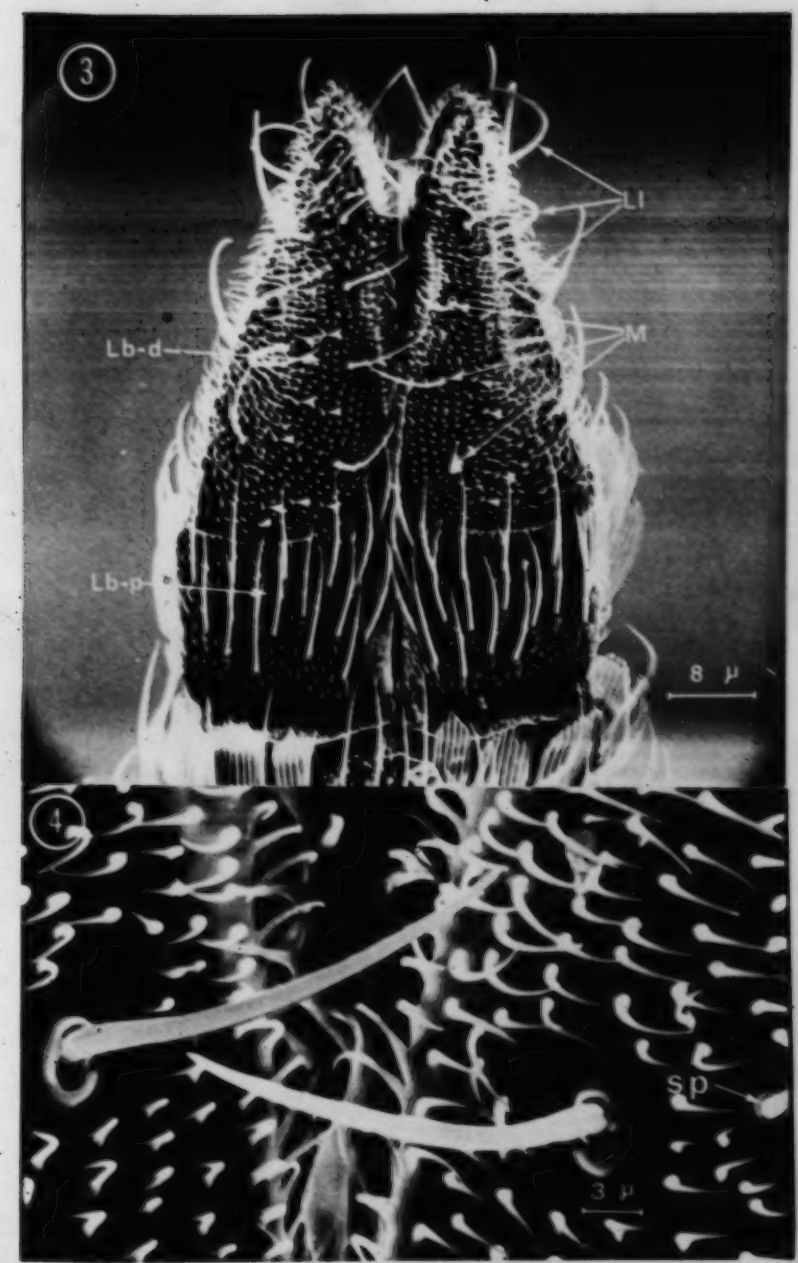


Fig. 3. Ventral aspect of female Aedes aegypti labella, showing the distal (Lb-d) and proximal (Lb-p) segments of the labella are joined transversely. Long labellar hairs (Ll), medium-sized hairs (M), and short papillae (arrow heads) are also found here. Note scales are almost absent on the proximal labellar segment.

Fig. 4. Same at higher magnification showing hair socket at the base of a short papilla (sp).

theca of the labium is important in protecting the fascicle by conserving the fascicular fluid and preventing it from drying. But Jones and Pilitt (1973) found that removal of the labella results in the failure of mosquitoes to penetrate the skin, again suggesting the importance of the labella as a guide during piercing.

1.1.1. Aboral Hairs

Aboral hairs on the distal segment of the labella are symmetrically arranged (Figs. 1-4). As already noted by Frings and Hamrum (1950), aboral hairs of Aedes aegypti can be classified into four different types according to their sizes: (1) long, pointed, socketed hairs averaging 40 μ in length, (2) medium-sized, socketed, blunt-tipped hairs between 20-30 μ long, (3) short, blunt, socketed papillae 4-6 μ long and (4) short microtrichia (Figs. 1-4). They reported that short papillae are present only on the dorsal surface of the labella. However, my SEM photographs show that these papillae are also present on the ventral surface (Figs. 3 and 4). Hairs on the proximal segment of the labellar lobes are all straight, socketed and have fine tips (Figs. 1, 3 and 6).

1.1.1.1. Long Labellar Hairs

Longitudinal ridges are found on the hair shaft of the long labellar hairs, but only a single cavity is found inside the hair lumen (Figs. 6-9). Each longitudinal ridge is finely scalloped on its surface (Figs. 7 and 8). A finely granulated substance is present inside the hair lumen. There is no evidence of any dendrites inside the lumen. Near the tip of the hair shaft, the lumen becomes smaller (Fig. 7), and it is very likely that these hairs do not have any opening to the outside. Crystal violet

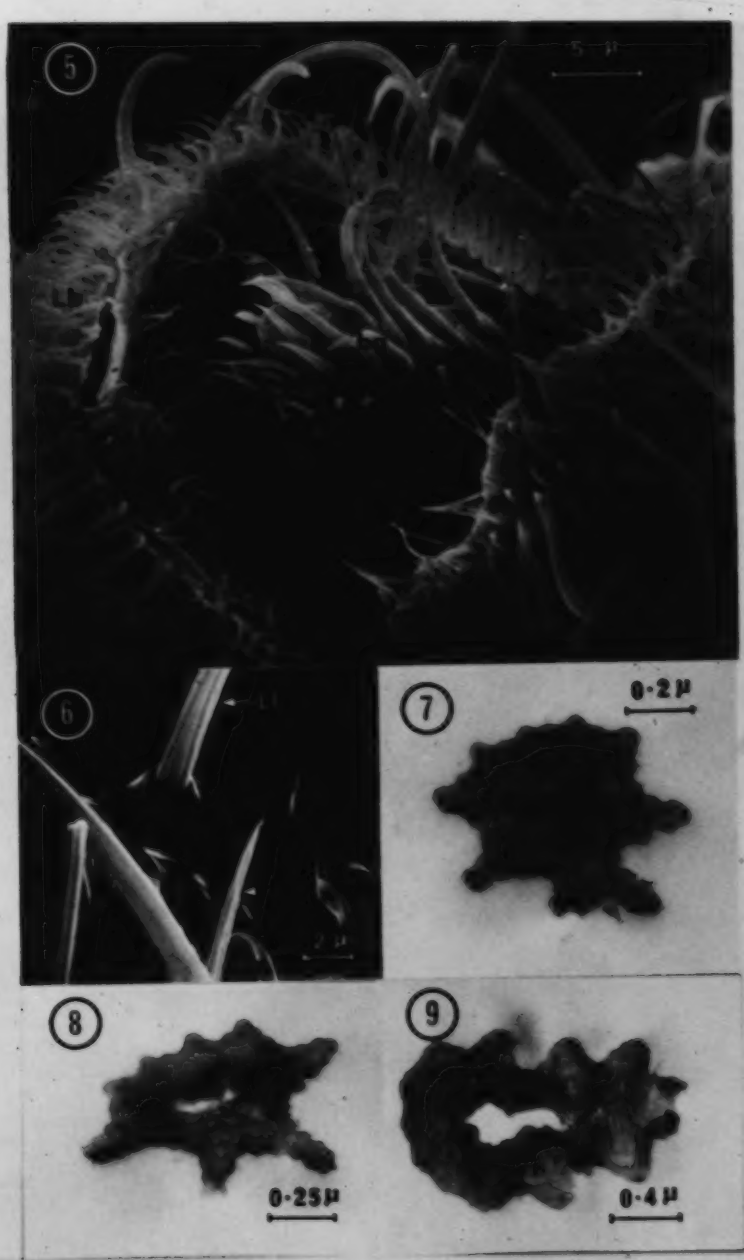


Fig. 5. Anterior top aspect of the tip of female Aedes aegypti labium, showing ligula (Lg) situated between the two labellar lobes (LB). Ligular hairs are not socketed at the base, and have smooth wall. Two apical hairs (Ap) extend out anteriorly through labellar folds at the tip.

Fig. 6. Long labellar hair (Ll) of male Aedes aegypti showing longitudinal ridges on the hair, and the sharp, pointed tip (arrow head) of labial hair.

Figs. 7-9. Transverse sections of long labellar hair of female A.aegypti.

Fig. 7. Near the tip of the hair. Longitudinal ridges on the hair appear as points of a "star".

Fig. 8. Section proximal to Fig. 7, showing a single central lumen of the hair. Each longitudinal ridge is finely scalloped on the surface.

Fig. 9. Same. Proximal to Fig. 8, near the base of the hair.

(Slifer, 1960) did not stain the tips of these hairs. Structurally, these hairs are very similar to the thick-walled hairs found on the antennal flagellum of Aedes aegypti described by Slifer and Sekhon (1962). A mechanoreceptive dendrite is found at the base of the long labellar hairs (Fig. 10). Whether this dendrite is attached to the hair base, or enters into the hair lumen for a short distance is unclear. Chaika and Elizarov (1971) reported that all aboral hairs of female Aedes aegypti are double-chambered, and they found no evidence of dendrites terminating at the base of the hair. Since they did not report any single-chambered hairs, the question remains whether this mechanoreceptive dendrite enters the hair lumen.

Behavioural studies showed that long labellar hairs respond to mechanical stimulation (Frings and Hamrum, 1950). But many workers (Zwonitzer, 1962; Feir et al., 1961; Owen, 1963, 1971; Owen et al., 1974) have found only double-chambered hairs, and they concluded that all aboral hairs beyond a certain length (e.g. 32 μ in Culiseta inornata as reported by Owen, 1963) are chemosensory. Consequently behavioural (Feir et al., 1961; Owen, 1963, 1971; Owen et al., 1974) and electrophysiological studies (Zwonitzer, 1969; Owen et al., 1974) were conducted on the long labellar hairs. However, Pearson (1970) using electrophysiological methods found that long labellar hairs are very sensitive to minute mechanical deflections which normally result in proboscis extension. He also found that it is very difficult to apply a chemical to a long labellar hair without evoking a response from the mechanoreceptor, and cautioned the use of proboscis movement as the criterion for positive response towards chemical stimulation.

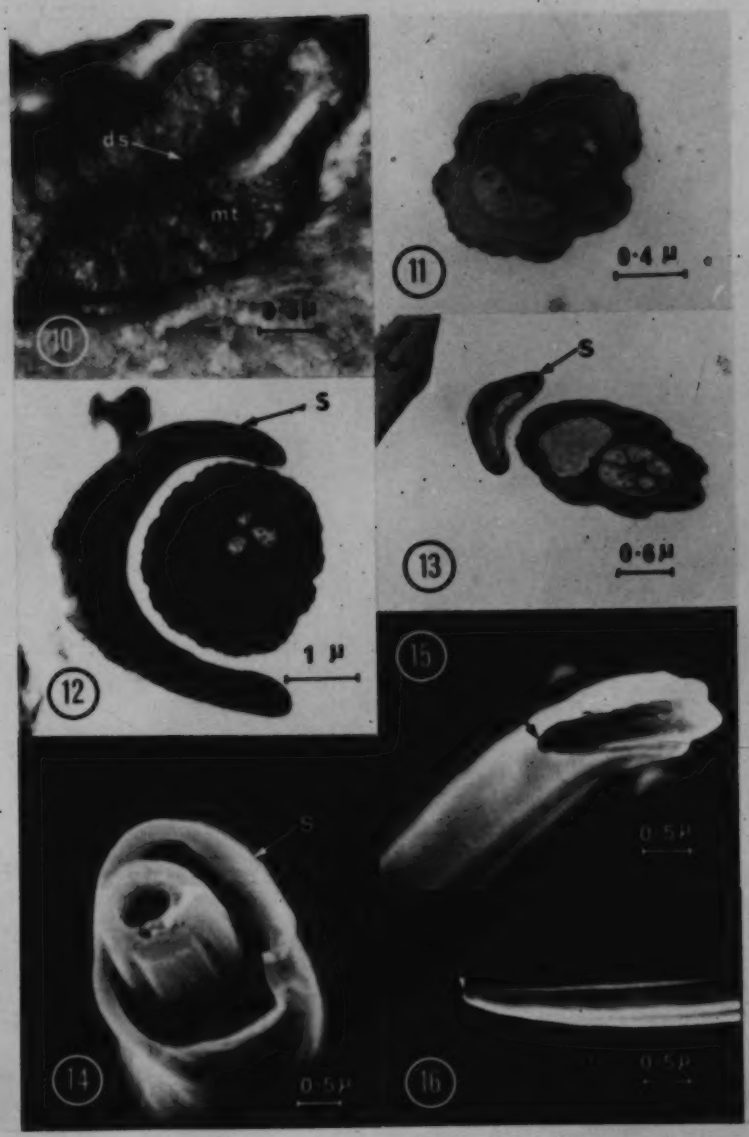


Fig. 10. Section near the base of a long labellar hair of female A.aegypti, showing microtubules (mt) of the mechanoreceptive dendrite enclosed by dendritic sheath (ds).
Figs. 11-13. Transverse sections of medium-sized labellar hairs of female A.aegypti. Each hair is double-chambered, with one chamber containing dendrites and the other a liquid with fine granules. Three to five dendrites are found in the circular chamber. S, hair-socket.
Fig. 14. A medium-sized labellar hair broken near the base on male A.aegypti labellum, showing longitudinal ridges on the hair shaft and two chambers inside the hair. S, hair-socket.
Figs. 15 & 16. Medium-sized labellar hairs of female A.aegypti, showing a drop of an unknown substance at the tip of the hair.

My morphological study supports his finding that the long labellar hairs are mechanoreceptors.

1.1.1.2. Medium-sized Hairs

These hairs are situated near the tip and on the dorsal and ventral aspects of the aboral surfaces of the labellar lobes. They are longitudinally grooved on the outside, and double-chambered inside. Three to five dendrites are present in one of the two chambers (Figs. 11-13). In some hairs containing three dendrites, three to four other dark, dendrite-like structures can be seen (Fig. 12). Whether these dark-staining structures are similar to the dark neurones described by McIver (1972) on the maxillary palps of female Aedes aegypti remains to be determined.

It is possible these are similar to the vesicles described by Zacharuk et al. (1971) in the antennal cone of A. aegypti larvae. They found that peripheral dendrites vesiculate laterally, and the vesicles were often attached to the dendrites. The difference here is that the vesicles they found are usually electron transparent.

With SEM, the double-chambered structure of the hair shaft can also be seen in broken medium-sized hairs (Fig. 14). The dendrite-free lumen of the hair shaft contains remnants of the trichogen cell, a condition similar to the blowfly labellar chemosensory hairs described by Dethier and Wolbarsht (1956). A substance is found at the tip of some medium-sized hairs (Figs. 15 and 16) which might be similar to the viscous droplets reported on the labellar and tarsal hairs of blowfly and stable-fly (Stürckow et al., 1967; Stürckow, 1967).

At the base of the medium-sized hairs, three to five dendrites are found inside the dendritic sheath (Figs. 17-19, 21). The dendritic sheath

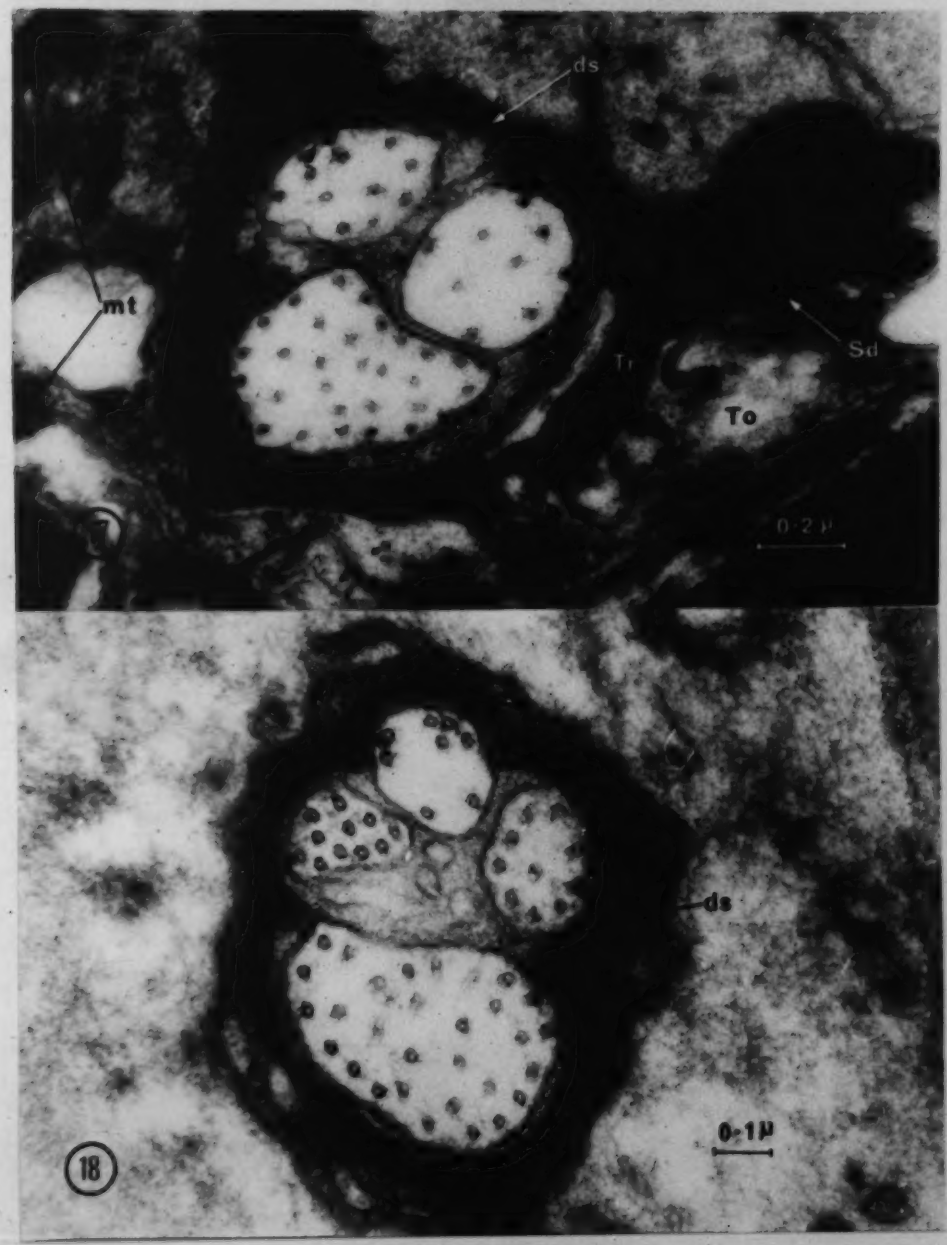


Fig. 17 & 18. Transverse section of medium-sized labellar hair sensilla proximal to the hair base.
Fig. 17. Sensillum with three dendrites. Dendritic sheath (ds) is enveloped by the trichogen cell (Tr). Microtubules (mt) are found in both trichogen and tormogen (To) cells. Septate-desmosomes (Sd) are found where the two cells come into contact.
Fig. 18. Sensillum with four dendrites. One of the dendrites show microtubular doublets. Note vesicle-like structures in between the dendrites. ds, dendritic sheath.

Figs. 19-21. Transverse section of medium-sized labellar hair sensilla proximal to the hair base in female Aedes aegypti.

Fig. 19. Sensillum with five dendrites. Dendritic sheath surrounding the dendrites almost disappear here. Microvilli (mv) are found on one side of the trichogen cell (Tr).

Fig. 20. A mechanoreceptive dendrite (D) inside the dendritic sheath (ds) is seen entering the hair lumen.

Fig. 21. Same as Fig. 19, but more proximal. Dendritic sheath has disappeared completely here. Microtubular doublets are found in all the dendrites. Microvilli are found on one side of the trichogen cell (Tr).

is surrounded by the trichogen cell, the latter in turn is enveloped by the tormogen cell (Figs. 17, 19, 21). Septate-desmosomes are found at the junction of the two enveloping cells (Fig. 17). At the ciliary region of one dendrite, it appears there are 9 + 1 microtubular doublets (Fig. 18), instead of the usual 9 + 0 configuration generally found in insect chemoreceptors (Slifer, 1970). However, since some doublets at the periphery of the dendrite are not as distinct as the central one, it is difficult to interpret the micrograph with certainty.

It is possible that this was due to the branching of the microtubules, and that one of the doublets was displaced into the centre. Multiplication of the microtubules through branching was reported in the earwig (Slifer and Sekhon, 1969) and mosquito larva (Zacharuk et al., 1971). Vesicles are found in between the dendrites, and microtubules are present in the extension of the trichogen cell that encloses the dendritic sheath (Fig. 18). Good fixation for mosquito labellar hairs is difficult to obtain. Similar difficulty was also encountered by Stürckow et al. (1973) in studying the labellar hairs of the blowflies.

Chaika and Elizarov (1971) reported one to five dendrites ascending into the lumen of the aboral chemosensory hairs in female Aedes aegypti. However, the reproduction of their micrographs was poor, and they did not show any sections of hair shafts containing less than three dendrites. In female Culiseta inornata, Zwonitzer (1962) using LM found three to four neurones associated with each aboral hair. Owen et al. (1974) using TEM found two types of sensory hairs on the aboral surfaces of C. inornata: one containing three dendrites and the other with five dendrites proximal to the base of the hairs, but only four dendrites in the hair shaft.

Results from behavioural studies have indicated that mosquito labellar hairs are sensitive to water, sugar solutions and unacceptable compounds (Frings and Hamrum, 1950; Hosoi, 1954; Owen, 1963, 1967, 1971; Salama, 1966; Feir et al., 1961; Owen et al., 1974). Electrophysiological studies have also shown that these hairs are stimulated by water, sugar, and NaCl (Zwonitzer, 1969; Owen et al., 1974). My study suggests that such responses may be mediated through the medium-sized hairs, which are double-chambered, and resemble the chemosensory hairs on the labella of blowfly (Grabowski and Dethier, 1954; Dethier, 1955). However, many medium-sized hairs are located more proximally on the labellar lobes (Figs. 2 and 3), and it is very likely that some will never touch the substrate during probing and piercing. Mosquitoes often spread their labellar lobes when the labellar hairs are stimulated with sugar solutions (Frings and Hamrum, 1950; Feir et al., 1961; Owen, 1963; Larsen and Owen, 1971) and unacceptable compounds (Salama, 1966). Such divarication will probably bring only some proximally located hairs into contact with the substrate, thus raising an interesting question as to the probable function of the more proximally located medium-sized hairs.

In the aquatic beetle Laccophilus maculosus, Hodgson (1953) found that sensilla basiconica on the tips of antennae are responsive to both gaseous and liquid stimuli. Thick-walled chemoreceptors sensitive to strong odours have been reported on the labellar hairs of the stablefly Stomoxys calcitrans (Hopkins, 1964) and on the legs of grasshoppers (Slifer, 1954, 1956). Recently, Dethier (1972) also found that chemoreceptors on the mouthparts and legs of the blowfly Phormia regina that normally respond to aqueous solutions also respond to compounds like organic and inorganic acids, and various nonpolar compounds in gaseous state. It is possible

that in mosquitoes, the more proximally located medium-sized hairs which do not normally come into contact with the substrate respond to vapours. But behavioural significance of these hairs is still unknown.

The number of dendrites found in the hair shaft agrees with the number found proximal to the hair base. It is likely then that there is no mechanoreceptive dendrite ending at the hair base. But inside the hair lumen one of the dendrites is always bigger than the rest and in most cases this large dendrite is partially isolated from the rest of the dendrites by the indentation of the dendritic sheath (Fig. 18), suggesting that this large dendrite might function as mechanoreceptor. A similar structure was described by Zacharuk and Blue (1971a) in the basiconic peg in the antenna of larval Aedes aegypti. In the blowfly Phormia regina and stablefly Stomoxys calcitrans, the labellar and tarsal chemosensory hairs have a mechanoreceptive dendrite terminating near the hair base (Grabowski and Dethier, 1954; Wolbarsht and Dethier, 1958; Adams et al., 1965).

The structure of the short papillae (sp, Figs. 2-4) in A. aegypti has yet to be studied. In female Culiseta inornata, Zwonitzer (1962) using LM called these sensilla basiconica, but was uncertain about the number of neurones associated with each papilla. Short microtrichia on the aboral surfaces are clearly not sensory.

1.1.2. Oral Papillae

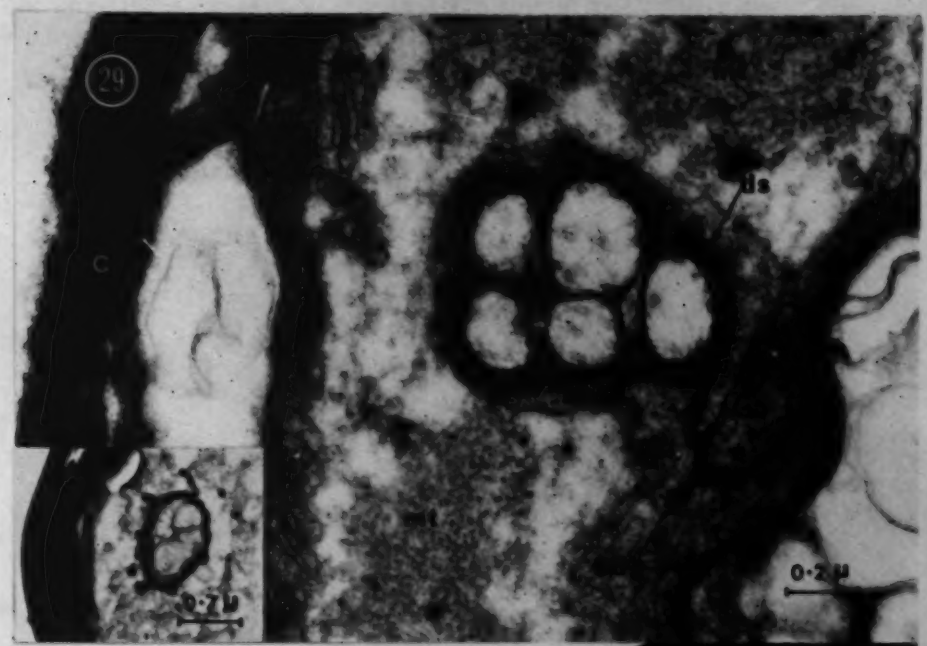
Six anteriorly directed, socketed papillae are found on the concave, oral surface of each labellar lobe (Fig. 22). On the dorsal and ventral oral surfaces, pseudotrachea-like structures are found, and oral papillae are sometimes found in between the microtrichia (Fig. 23).

Fig. 22. Oral papillae (Op) on the oral surface of female A.aegypti labella. Note the papillae have smooth outer surface.
Fig. 23. Same of male A.aegypti showing pseudotrachea-like structure (Ps) on the dorsal and ventral oral surfaces of the labellum. Op, oral papillae.
Fig. 24. Higher magnification of Fig. 23, showing an opening (arrow) at the tip of one oral papilla.
Fig. 25. Vital methylene blue stained female Culiseta inornata labellum, showing dendrites entering through hair socket (S) into the lumen of the papilla (P). The dendrites are constricted just below the socket (arrow), where the ciliary region of the dendrites are probably located.
Figs. 26 & 27. Transverse sections of oral papillae with three and four dendrites.
Fig. 28. Transverse section of an oral papilla near the base, showing five dendrites surrounded by dendritic sheath (ds). One of the dendrites is bigger than the rest (arrow), probably a mechanoreceptive dendrite. Note the dendritic sheath has separated from the wall of the papilla here.

Vogel (1921) suggested that these pseudotrachea function in a manner similar to the suction cups on the toes of the gecko, providing a strong hold on the skin of the host during biting and sucking. Robinson (1939) pointed out that Vogel's suggestion has no backing. However, Vogel was probably the first to notice the oral papillae in mosquitoes. He called them sensilla basiconica, and considered them to be shortened tactile bristles. Zwonitzer (1962) found six of these papillae in female Culiseta inornata, and also called them sensilla basiconica. Larsen and Owen (1971) referred to these papillae as sensilla trichodea. Since these sense organs are papilla-like, and are present on the oral surfaces of the labella, I call them oral papillae in this study.

An opening approximately 0.15 μ in diameter is found at the tip of the papilla (Fig. 24). Vital methylene blue staining of the labella of both sexes of Aedes aegypti and Culiseta inornata showed that these papillae have dendrites entering the lumen which extend to the tip (Fig. 25). TEM sections show that the papillae are double-chambered, with three to five dendrites inside the big chamber. The dendrites are enclosed in a dendritic sheath (Fig. 26-28). Proximal to the base of the papillae, three to five dendrites are enclosed in a dendritic sheath, the latter enveloped by the trichogen and tormogen cells (Figs. 29 and 30). I found no evidence of mechanoreceptive dendrite terminating near the base of the papillae. Septate-desmosomes are found between the junction of the trichogen and tormogen cells (Fig. 29).

In C. inornata, Larsen and Owen (1971) also found that the oral papillae are double-chambered. Their micrograph shows five dendrites enclosed in a dendritic sheath proximal to the base of the papilla. In the blowfly Phormia regina, Larsen (1963) found four dendrites in the



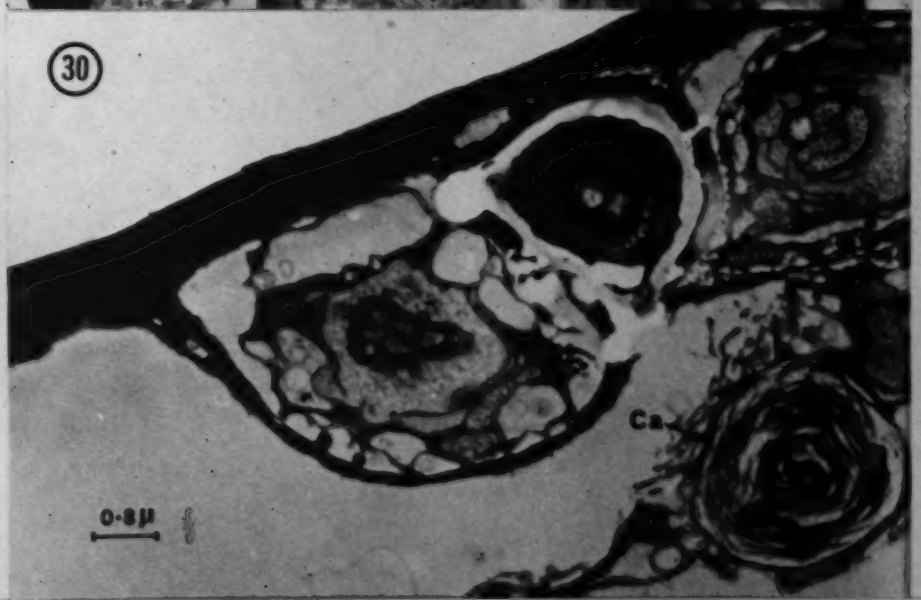


Fig. 29. Transverse section of an oral papilla sensillum proximal to the base in female Aedes aegypti showing five dendrites. Microtubules are found in the trichogen cell surrounding the dendritic sheath (ds). Septate desmosomes (Sd) are found at the junction between the trichogen and tormogen cells. Inset : Same, with three dendrites. Vesicles are found along the inside wall of the dendritic sheath.

Fig. 30. Section of a labellum showing three oral papillae with three to five dendrites, and the cap (Ca) of a labellar chordotonal organ.

interpseudotracheal papillae of the labella, and noted that the dendritic sheath does not fuse with the wall of the papilla. Tominaga et al. (1969) reported in the fleshfly Boettcherisca peregina that each interpseudotracheal papilla has three chemoreceptive dendrites entering the lumen of the papilla, and one mechanoreceptive dendrite ending at the base. They also noted that these papillae are single-chambered. In A. aegypti, if there is any mechanoreceptive dendrite associated with the oral papillae, such a dendrite instead of terminating near the base of the papilla, probably enters the papillar lumen for a short distance (Fig. 28).

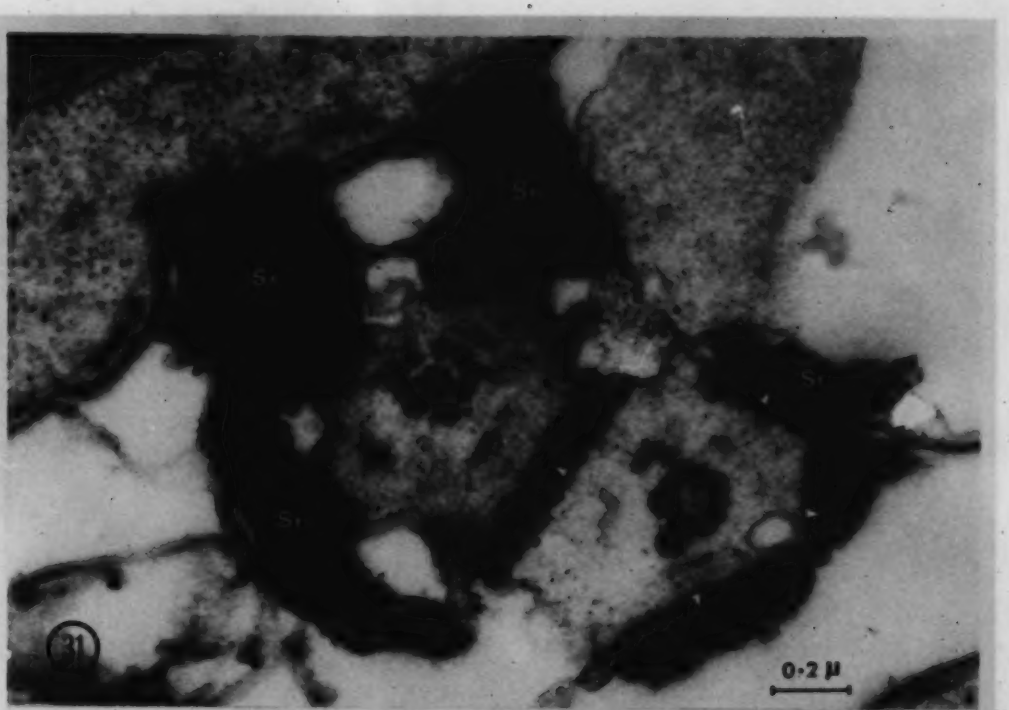
Larsen and Owen (1971) found in Culiseta inornata that when chemosensory hairs on the labella are placed in contact with water or sugar solution, the labellar lobes spread apart, thus permitting the ligula to come into contact with the test solution, causing the ligula to increase by 76.65% of its original size. Consequently the test solution will probably spread over the ligular surface and make contact with the oral papillae. They suggested that it is probably through this mechanism that the mosquito mediates sucking of water and sugar solution. Whether such a mechanism exists in A. aegypti remains to be investigated. In male A. aegypti, the oral and ligular surfaces are very close to each other, leaving only a small space in between (see Fig. 10 of Lee, 1974). Solutions that come into contact with the tip of the labellar lobes can probably reach the oral papillae through capillary action.

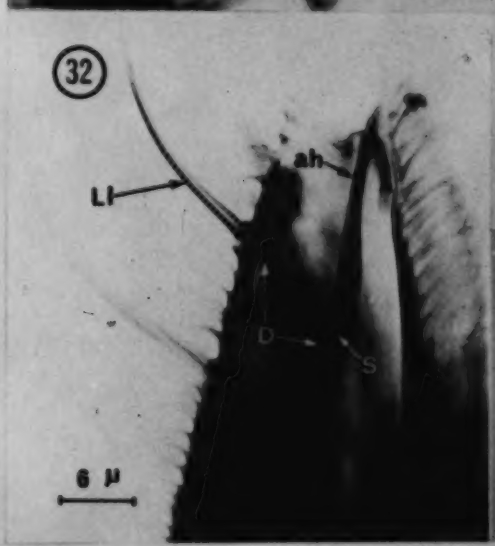
Four to five oral papillae arranged in two rows are also present on the oral surface of the labella in adult chaoborid Chaoborus americanus (personal observation).

1.1.3. Chordotonal Organ

Inside each labellum, a chordotonal organ with two sensory cells associated with it is situated close to the oral papillae (Figs. 30 and 31). At the ciliary region of the sensory cells, the cells are surrounded by six scolopale rods (Fig. 31). Desmosomes are found between the cell membrane of the sensory cells, and also between the sensory cell membrane and scolopale rods (Fig. 31). At the distal end of the chordotonal organ, only a single cap is present, which is surrounded by concentric layers of fibrous elements (Fig. 30). I was unable to determine the distal attachment of the chordotonal organ using TEM, because of a lack of serial sections. From LM sections, it seems the cap is attached to the oral surface, at a region slightly anterior to the oral papillae.

This is the first report of chordotonal organs in the mosquito labellum. It is similar to the chordotonal organ described in the legs of the shore crab Carcinus maenas (Whitear, 1960, 1962), and also to the Johnston organ scolopidium of Drosophila melanogaster (Uga and Kuwabara, 1965), in having two sensory cells associated with one chordotonal organ. However, in the mosquito, at the ciliary region of the sensory cells, the two cells are separated by cell membranes, whereas in the shore crab and fruitfly, the ciliary segments are inside the scolopale without any membrane separating them. The presence of desmosomes in chordotonal organ were also reported in the tympanal organ of locust (Gray, 1960) and in the legs of shore crab (Whitear, 1962). They also found septate-desmosomes at various parts of the chordotonal organs. Zacharuk and Blue (1971b) also found a chordotonal organ with a single nerve cell within the antennal cone of larval A. aegypti, and suggested that it functions either as a stretch receptor, or as a monitor for low frequency vibration in the adjacent aquatic environment.





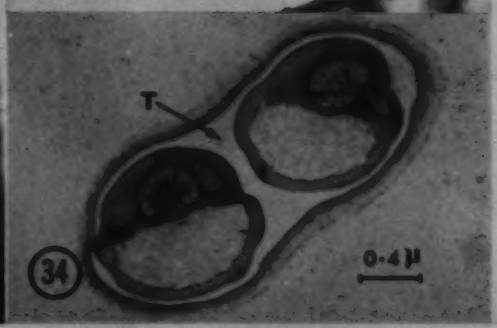


Fig. 31. Transverse section of labellar chordotonal organ showing electron-dense scolopale rods (Sr) surrounding two sensory neurones. Desmosomes (arrow heads) are found at the junction between the two sensory neurones, and also between the scolopale rods and the sensory neurones.

Fig. 32. Vital methylene blue stained labellum of female Culiseta inornata, showing dendrites leading to the long labellar hair (Ll) and apical hair (ah). S, socket.

Fig. 33. Transverse section of two apical hairs near the hair tip. Each hair has two chambers, and five dendrites are found in one of the chambers.

Fig. 34. The apical hairs extend from inside the labellar lobe to the outside through a "tube" (T). The number of dendrites here is four for each hair.

Behavioural studies have shown that mosquitoes often spread their labella when the labellar hairs are stimulated with sugar, water, and unacceptable compounds (see p. 17 for citation). But when mosquitoes are feeding on blood, the two labellar lobes are firmly appressed against each other (Robinson, 1939; Gordon and Lumsden, 1939; Jones and Pilitt, 1973). Dr. W. Horsfall of the Department of Entomology, University of Illinois at Urbana, Illinois, U.S.A., has made a film on the feeding behaviour of female A. aegypti on the footweb of a frog, and he kindly loaned me the film for study. I also noted that the two labellar lobes were closely held against each other during the whole process of feeding on the host. Chordotonal organs are generally recognized as stretch receptors. Whitear (1960, 1962) suggested that in chordotonal organs where each scolopidium is associated with two sensory cells, one sensory cell probably respond to stretching, and the other to slackening of the cap. The chordotonal organ in the mosquito labellum probably functions to monitor the spreading and closing of the labella during feeding. Both flexor and extensor muscles are present in the labella of mosquitoes (Christophers, 1960).

1.1.4. Apical Hairs

Inside each labellum, there are usually two hairs deeply invaginated in the lobe. These hairs emerge anteriorly through longitudinal "tubes", and project out between the folds at the tip of the labellum (Fig. 5). Near the distal end of the labellum, the two hairs share a common "tube" for a short distance (Fig. 34), but proximally, each hair is enclosed by a separate "tube" (Fig. 35). Vital methylene blue staining shows that these hairs are socketed at the base, with dendrites entering the hair

Fig. 35. Transverse section of an apical hair near the hair-socket (S) in female Aedes aegypti. A third lumen appears here, which is probably the extension of the trichogen cell sinus. Note five dendrites are found here.

Fig. 36. Transverse section of two apical hair sensilla proximal to the hair base. Five dendrites are found inside the dendritic sheath, the latter is enveloped by the trichogen cell (Tr). Two large vacuoles filled with electron dense material are associated with the tormogen cell (To).

lumen and extending to the tip of the hairs (Fig. 32). TEM sections of these hairs show that these hairs are double-chambered, with the smaller chamber containing five dendrites (Fig. 33). Near the base of the hair, besides the two lumina found at the distal end of the hair shaft, a third lumen appears (Fig. 35). This third lumen is probably the trichogen cell sinus. The dendritic sheath surrounding the dendrites becomes very distinct at this region. Proximal to the hair base, the dendritic sheath is enveloped by trichogen and tormogen cells, and the trichogen cell encloses the trichogen cell sinus (Fig. 36). The axons of these dendrites later join the labial nerve. As the number of dendrites at the hair tip is the same as that proximal to the hair base, and I could not find any evidence of a dendrite ending near the hair base, it is possible these apical hairs do not have a mechanoreceptive dendrite. Not all the five dendrites found in the hair shaft extend to the tip of the hair. In some sections at the distal end of the hair, only four dendrites are found (Fig. 34). The number of apical hairs in each labellum is usually two, but in some specimens, three apical hairs are found.

Transverse sections of the apical hairs can be seen in Figs. 5a and 6 of Vogel (1921), but he labeled them as sensory cells. Zwonitzer (1962) also noted these apical hairs in female Culiseta inornata, but wrongly reported that they project anteriorly at the tip of the labellum in the same plane as the oral papillae.

Structurally, the apical hairs can be classified as thick-walled chemoreceptors. They differ from the medim-sized, aboral labellar hair in having a smooth outer wall. Since the apical hairs are so located that they will come into contact with the substrate when the mosquito is probing on the host, these hairs may be involved in the discrimination of the host.

1.1.5. Ligular Hairs

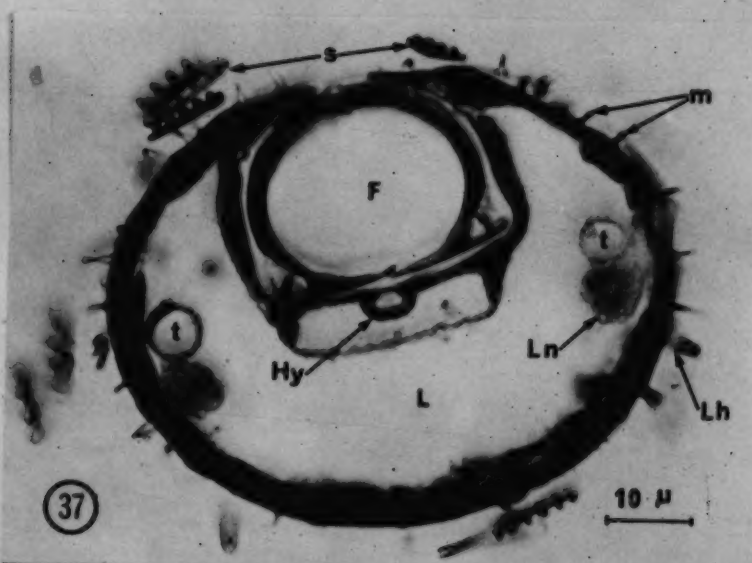
Cuticular hair-like projections covering the ligula in Aedes aegypti are not socketed at the base (Fig. 5). Each projection has a single lumen inside, but is devoid of any sensory structure. Transverse sections of the ligula also do not show any nervous tissue inside. Therefore a non-sensory function can be assigned to them.

Owen (1963) reported from his behavioural studies using Culiseta inornata and Aedes dorsalis that ligular hairs are chemosensory and respond to water and sucrose. Later Larsen and Owen (1971) found that ligular hairs in C. inornata are not chemosensory, and suggested that the behavioural response observed by Owen (1963) was probably a result of the oral papillae coming into contact with the ligular surface which was coated with the test solution.

1.2. Labial Hairs

Proximal to the labella, the outer surface of the labium is covered with scales, hairs and microtrichia (Figs. 1, 3, 37, and 38). Pearson (1970) using LM, found that the labial hairs of female A. aegypti are innervated. Using vital methylene blue staining, I found that there is one nerve cell associated with each hair, suggesting that these hairs are probably mechanoreceptors. LM sections of the labium showed that these hairs have only a single lumen in the hair shaft (Fig. 37).

At the base of the labium, six to eight long socketed hairs are found on the ventral surface of the labium (Fig. 38). These hairs have sharp, pointed tips, with longitudinal grooves on the outer hair wall (Fig. 39), similar to the long labellar hairs. Whether these hairs are



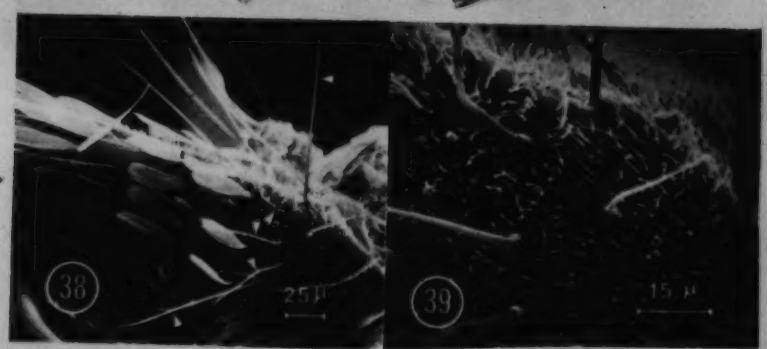


Fig. 37. Transverse section through the labium of male Aedes aegypti. F, food canal; Hy, hypopharynx; L, labium; Lh, labial hair; Ln, labial nerve; m, microtrichia; t, tracheal tube.
Fig. 38. Hairs at the base of male Aedes aegypti labium (arrow heads).
Fig. 39. Higher magnification of Fig. 38, showing socketed, longitudinally grooved labial hairs among the microtrichia.

innervated has yet to be studied. However, their external morphology suggests that they are probably mechanoreceptors.

When a mosquito is feeding on a host, as the fascicle enters the host tissue, the labium becomes bent gradually, to a point where the labium almost becomes double under the head as the fascicle penetrates deeper. During such bending of the labium, hairs at the base of the labium may touch the ventral side of the head. After feeding, the fascicle is gradually eased back into the labial theca during withdrawal of the fascicle from the host tissue, and the labium is observed to rock from side to side (see Gordon and Lumsden, 1939, and Jones and Pilitt, 1973, for a detailed description of such behaviour). As the labium straightens, hairs at the base of the labium may lose contact with the ventral side of the head. Therefore these labial hairs are probably involved in providing information to the mosquito about the "state" of bending of the labium during and after feeding. Schiemenz (1957) also noted a transverse row of seven hairs at the base of the labium in Culiseta (=Theobaldia) annulata, and suggested that these hairs probably play a role as tactile hairs in the bending of the labium during piercing and sucking. Christophers (1960) found in A. aegypti that the number and arrangement of these hairs are more regular in the females than in the males.

2. Fascicular Stylets

2.1. Labrum

The structure and function of the labrum and labral sense organs in different species of mosquitoes have been studied by many workers. Von Gernet and Buerger (1966) and I (Lee, 1974) have already reviewed this subject extensively. In the present study, I examined the labra of both sexes of 40 species of mosquitoes belonging to 15 genera using SEM, and 10 species using LM (Appendix A). The primary purpose was to investigate any differences between the labra of blood-sucking and nonblood-sucking mosquitoes. Whenever possible, I tried to locate the opening of the apical and subapical sensilla using SEM. The dorsal wall of the labrum was also examined in some species.

In the following description, I use the same terminology for the labral sense organs as Lee (1974). I attempted to measure the size of the apical and subapical sensilla using SEM. However, since the specimens were often tilted at different angles in the pictures, foreshortening makes an accurate measurement very difficult, and the angle of tilt cannot be estimated because of the great depth of field of the SEM. Consequently the measurements given below can only be considered as rough estimates.

2.1.1. Labral Sense Organs

2.1.1.1. Apical Sensilla

In female mosquitoes, the apical sensilla are located at the tip of the labrum. The sensilla resemble fine, pointed finger nails (Figs. 44, 47-50). They are absent in all the male mosquitoes examined. Instead, in most of the male mosquitoes I have studied, the tip of the

Fig. 40. Scanning electron micrograph of the tip of male Toxorhynchites rutilus labrum.
Fig. 41. Same of female T. rutilus.
Fig. 42. Same of male Toxorhynchites brevipalpis. Arrow points to the dorsal longitudinal groove.
Fig. 43. Same of female T.brevipalpis.
Fig. 44. Apical sensilla on the labrum of female Culex declarator. Arrow head points to the opening of the sensillum.
Fig. 45. Same of female Trichoprosopon digitatum showing the opening of the apical sensillum.

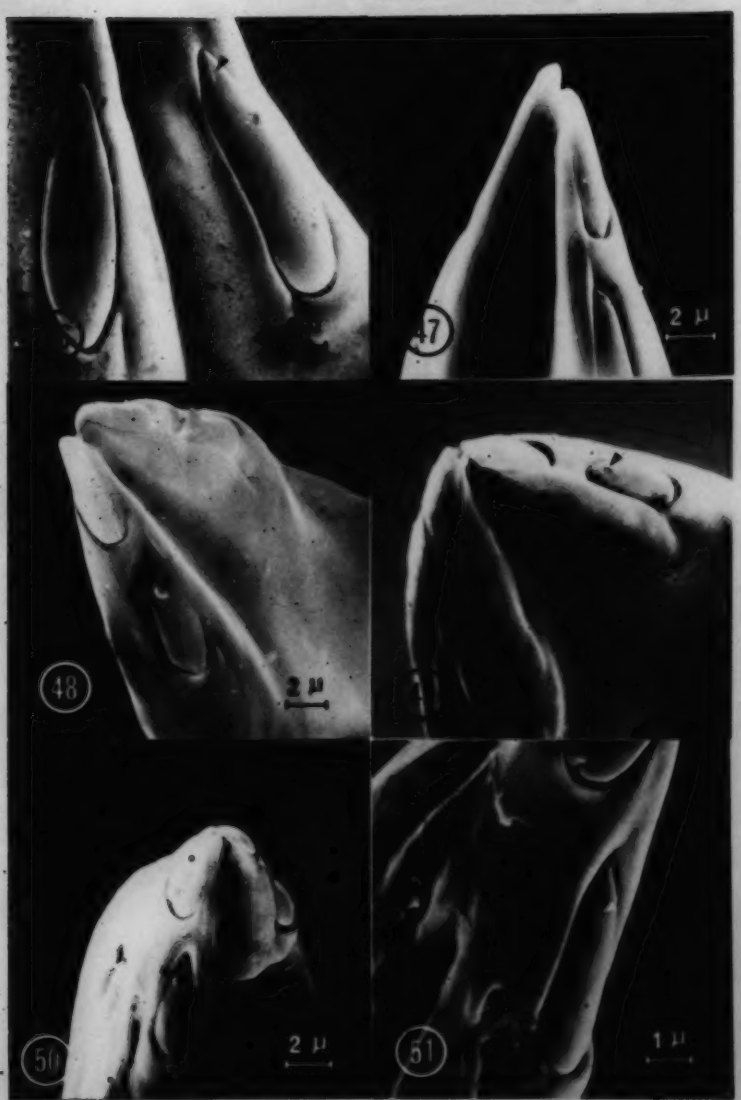


Fig. 46. Ventral aspect of female Wyeomyia smithii labrum showing the opening of the subapical sensillum (arrow head).
Fig. 47. Same of female Culiseta inornata. Arrow head points to the opening of the subapical sensillum.
Fig. 48. Lateral top aspect of female Trichoprosopon digitatum showing the "papilla" on the opening of the subapical sensillum (arrow head).
Fig. 49. Same of female Aedes excrucians. Note the "papilla"(arrow head) on the subapical sensillum.
Fig. 50. Same of female Aedes pionips. Note the longitudinal groove on the apical sensillum, and the "papilla" on the subapical sensillum (arrow head).
Fig. 51. Subapical sensillum of the same specimen as Fig. 50, except this one was taken from the other side of the labrum. Note the opening of the sensillum (arrow head).

labrum is forked (Figs. 58, 60, 65, 72, 76, 77, 79) with the following exceptions. In Anopheles stephensi and A. merus, the tip of the labrum is slightly forked, and in A. earlei, A. albimanus and A. farauti and Opifex fuscus, the tip of the labrum is not forked (Figs. 53, 54, 78).

Apical sensilla are absent in both sexes of Toxorhynchites rutilus and T. brevipalpis. In T. rutilus, the labral tip is forked (Figs. 40, 41), whereas in T. brevipalpis, it is many-pointed (Figs. 42, 43). These sensilla are also absent in T. splendens (von Gernet and Buerger, 1966). It seems the absence of apical sensilla in this genus is related to feeding habits, as the adults of this genus feed only on plant nectar (Muspratt, 1952). However, apical sensilla are found in Wyeomyia smithii and Opifex fuscus (Figs. 59, 84) which are not known to feed on blood (See Price, 1958 for W. Smithii and Horsfall, 1955 for O. fuscus), and also in the autogenous strain of Aedes atropalpus.

The length of the apical sensilla ranges from 5 to 13 μ in most species, and in Uranotaenia lowii, these sensilla average only 3 μ long. The outer wall of the sensillum is usually smooth (Figs. 44, 45, 47). In Anopheles earlei and some Aedes species, a longitudinal groove is found along the outer margin of the sensillum (Figs. 50, 51), as in Aedes aegypti (Lee, 1974). The opening of these sensilla is difficult to find using SEM. A single opening near the tip of the sensillum was observed only in a few specimens out of approximately 200 SEM preparations of female labra belonging to different species. In Culex declarator and Anopheles earlei, the opening is in a little depression (Fig. 44), whereas in Trichoprosopon digitatum, a tiny plug is present inside the depression (Fig. 45). In female A. aegypti, I found that the apical sensilla have five dendrites inside the lumen of the sensillum extending to the apical opening, resembling thick-walled chemoreceptors (Lee, 1974).

2.1.1.2. Subapical Sensilla

These are present in all the female mosquitoes examined, except in Toxorhynchites species and in male mosquitoes (Figs. 41, 43). They are situated behind the apical sensilla, and most of them are either lateral or ventro-lateral in position (Figs. 47-51). In W. smithii, these sensilla are ventral in position (Figs. 46, 59). The length of the sensilla ranges from 5 to 12 μ. An opening slightly behind the tip of the sensillum is seen in most of the species. In some preparations, the opening appears to be on a small papilla (Figs. 49, 50), but in others, the opening is in a depression (Figs, 46, 47). Trichoprosopon digitatum has the biggest papilla among the species examined (Fig. 48).

In a single preparation of Aedes pionips, I found a papilla on one sensillum, and a depression on the sensillum on the other side (Figs. 50, 51). Since these sensilla are structurally very similar to the chemosensory hairs on the labella and tarsi of the blowflies in having two lumina in the sensillum (Lee, 1974), it is possible that the papilla is formed by a substance secreted by the sensillum. Stürckow (1967a, b) reported that the chemosensory hairs on the tarsi and labella of the blowflies secrete a viscous fluid through the tip opening.

The subapical sensilla in Wyeomyia smithii, Opifex fuscus and Aedes atropalpus are morphologically similar to those in the mosquitoes that feed on blood. In mosquitoes that had blood-fed once, I could find no visible damage to either apical or subapical sensilla.

Structurally, the subapical sensilla can be classifed as thick-walled chemoreceptors (Lee, 1974).

2.1.1.3. Labral Ridge Receptors

I first reported these receptors in both sexes of Aedes aegypti

(Lee, 1974). Whether these receptors are also present in the mosquitoes studied here has yet to be determined using TEM.

2.1.1.4. Campaniform Sensilla

These are generally located ventro-laterally near the opening of the labral food canal in both sexes of mosquitoes. Von Gernet and Buerger (1966) reported that they found a peg projecting from the centre of the sensillum only in some species. In this study, I found that a peg is always present wherever a campaniform sensillum (c.s.) is found. The location of the c.s., and the shape of the cap-membrane is different in different species of the same genus, and even among individuals of the same species.

In male Anopheles species, the position of the c.s. varies between species. In A. earlei, A. stephensi and A. merus, the c.s. are located on the antero-lateral edges of the labrum, and in A. stephensi, each c.s. is "guarded" by a cuticular projection (Fig. 52). In A. albimanus, the anterior lateral edges of the labrum have extended forward, and the c.s. are located laterally inside (Fig. 53). In A. farauti, the c.s. are on the tip of the lateral edges of the labrum (Fig. 54).

In female Anopheles mosquitoes, the c.s. are situated on the roof near the opening of the labral food canal in A. earlei and A. farauti (Figs. 55, 56). In A. earlei, one c.s. is positioned slightly anterior to the other (Fig. 55). In A. albimanus, A. stephensi and A. merus, the c.s. are located laterally (Fig. 57).

The cap-membrane in both sexes of Anopheles species examined is usually dome-shaped (Figs. 52-54, 56, 57). In A. earlei, the cap-membrane is peg-like, which could be due to shrinkage because of poor fixation,

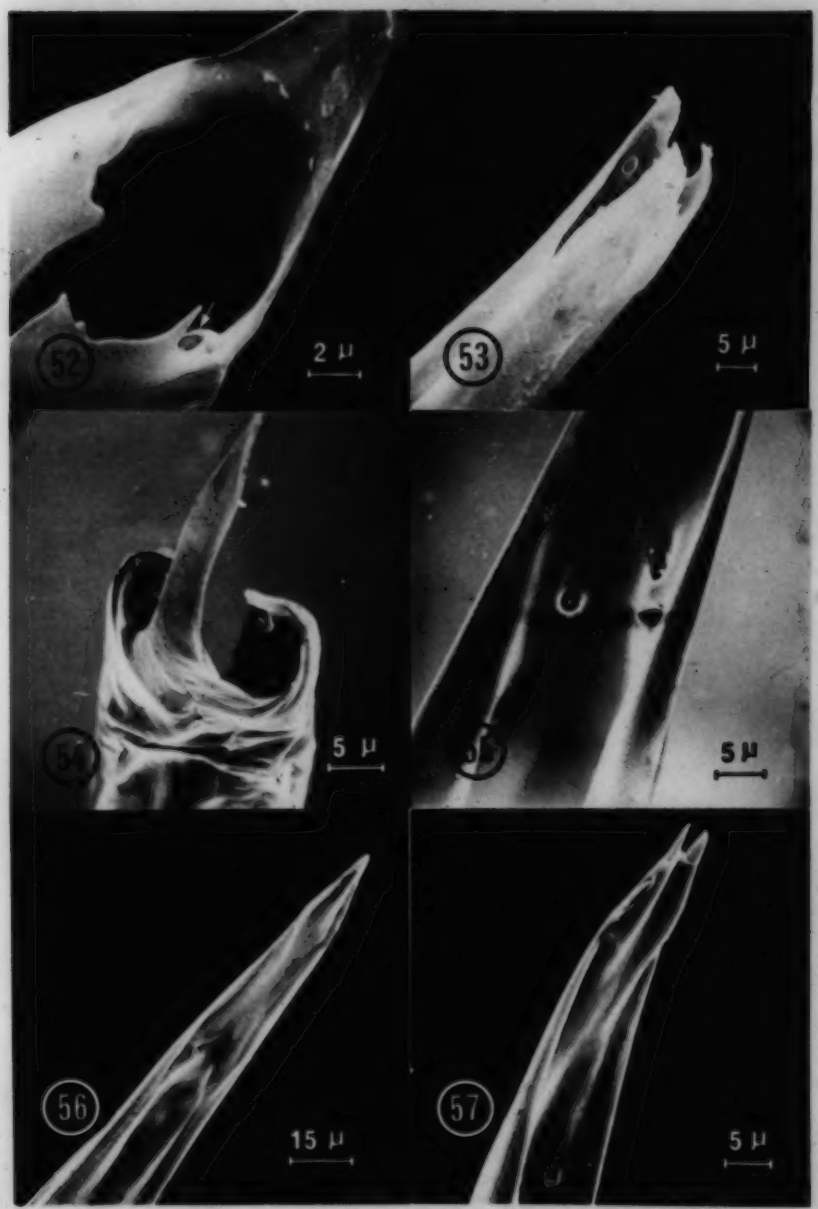


Fig. 52. Campaniform sensillum (arrow) of male Anopheles stephensi. Note the "guard" beside the sensillum.
Fig. 53. Same of male Anopheles albimanus.
Fig. 54. Same of male Anopheles farauti.
Fig. 55. Same of female Anopheles earlei.
Fig. 56. Same of female Anopheles farauti.
Fig. 57. Ventro-lateral aspect of female Anopheles merus labrum.

where the cap-membrane has collapsed on the tubular body underneath (Fig. 55).

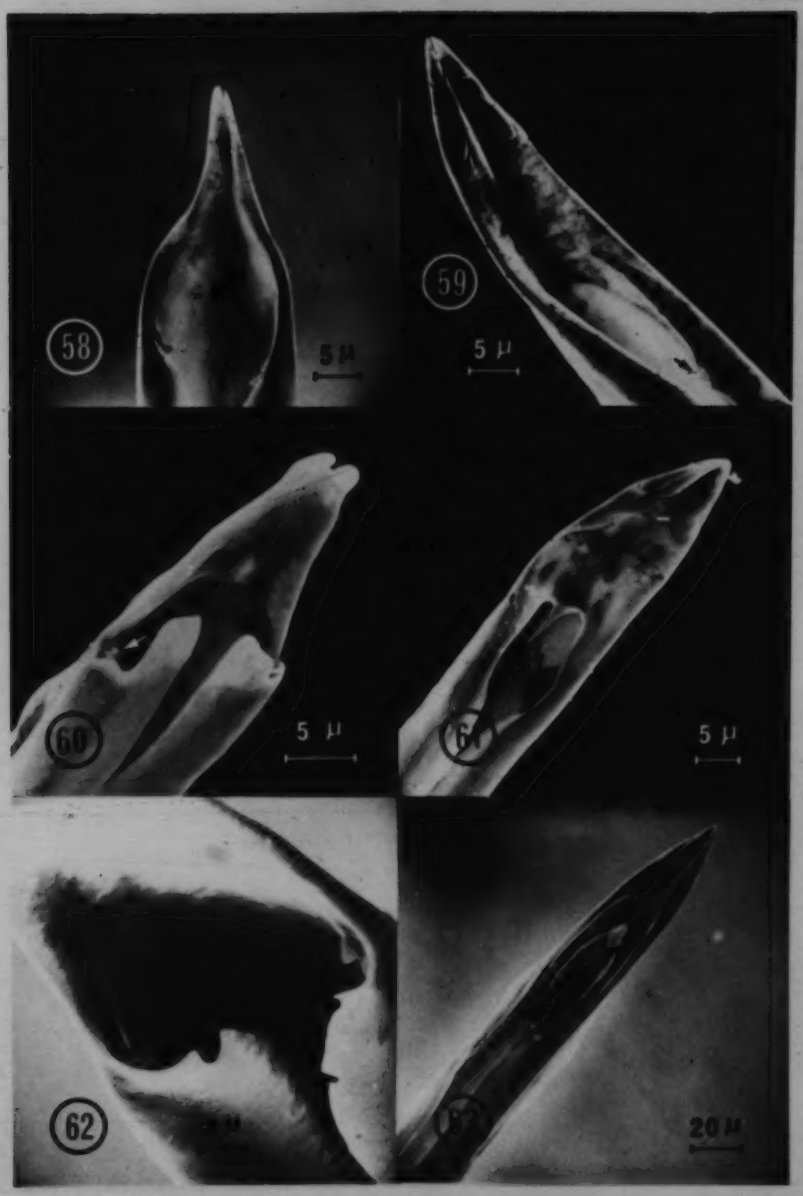
C.s. are absent in the two species of Toxorhynchites I have studied (Figs. 40-43). They are present in both sexes of T. splendens (von Gernet and Buerger, 1966).

In both sexes of Wyeomyia smithii, the c.s. are situated near the food canal opening on the lateral walls (Figs. 58, 59). The cap-membrane is conical in shape in both sexes. Hudson (1970) missed these sensilla in her SEM study of this species.

The c.s. in male Uranotaenia lowii are located on the indented lateral labral wall, facing anteriorly (Fig. 60). In the females, a median ridge on the roof of the labrum forms a partial partition between the two c.s., and the cap-membrane is conical in shape (Fig. 61).

In male Psorophora species, the c.s. are situated laterally as in male W. smithii, and the cap-membrane is conical in shape (Fig. 62). But in the females, part of the inner dorsal labral wall is split medially, and the c.s. are located along the edges of the median split (Figs. 63, 64). The socket of the c.s. is sickle-shaped (Fig. 64). Such median fissure on the labrum was not shown by Waldbauer (1962) in his drawing of female Psorophora ciliata labrum.

In Trichoprosopon digitatum, Coquillettidia perturbans, Orthopodomyia signifera, Eretmapodites chrysogaster, Opifex fuscus, Aedes, Armigeres, and in Culiseta species, the c.s. in the males are positioned laterally on the edge of the labral opening (Fig. 65), whereas in females, the c.s. are situated laterally inside the lateral labral walls (Fig. 66). The shape of the cap-membrane is variable in different species, and even among individuals of the same species. In most of these species, the cap-



Figs. 58-63. Campaniform sensilla on the labrum of male and female mosquitoes. Arrows or arrow heads point to these sensilla.
Fig. 58. Male Wyeomyia smithii.
Fig. 59. Female W.smithii.
Fig. 60. Male Uranotaenia lowii.
Fig. 61. Female U. lowii.
Fig. 62. Male Psorophora varipes.
Fig. 63. Female P. varipes.

membrane is either conical (Figs. 66, 69) or peg-like (Figs. 67, 68). The cap-membrane in some Aedes species have a notched tip (Fig. 65, arrow). In Culiseta species, the cap-membrane in some specimens is truncated at the apex (Fig. 70). In male Culiseta melanura, the cap-membrane of the c.s. is peg-like in some (Fig. 68), but conical in others (Fig. 69). Whether such variation is a fixation artifact has yet to be determined.

In both sexes of Culex mosquitoes and in Deinocerites pseudes, the c.s. are not found near the opening of the food canal (Fig. 71), as in the species described above, but are inside the food canal (Figs. 72, 73). Such similarity between the two genera probably reflects their close phylogenetic relationship, as pictured by Ross (1951). Von Gernet and Buerger (1966) and Froelich (1971) have also noted that in Culex mosquitoes, the c.s. are located some distance away from the tip of the labrum. These sensilla are situated ventro-laterally inside the food canal, and are symmetrically arranged in D. pseudes and some Culex mosquitoes. But in some Culex mosquitoes, often one c.s. is situated a little anterior to the other (Fig. 74), as in Anopheles earlei (Fig. 55). Such asymmetrical arrangement of the sensilla is independent of the sex and species in Culex, and there is no definite pattern regarding the relative position of the two c.s. The shape of the cap-membrane is always conical (Fig. 75). From LM measurements, the socket diameter of the c.s. in Culex mosquitoes is between 2 and 2.5 μ, and that of male D. pseudes averaged 4.3 μ and 3.5 μ in the female.

The average distance of the c.s. from the tip of the labrum, and the relationship of this distance to the length of the whole labrum are summarized in Table I. The position of the c.s. in female species in

Figs. 64-69. Labral campaniform sensilla (c.s.).
Fig. 64. Higher magnification of Fig. 63 showing the c.s.
Fig. 65. Male Aedes excrucians. The cap-membrane in one c.s. has a notched tip (arrow).
Fig. 66. Female Eretmapodites chrysogaster. Arrow head points to the c.s.
Fig. 67. Female Aedes communis.
Fig. 68. Male Culiseta melanura.
Fig. 69. Same as Fig. 68. Note the difference in the shape of the cap-membrane.

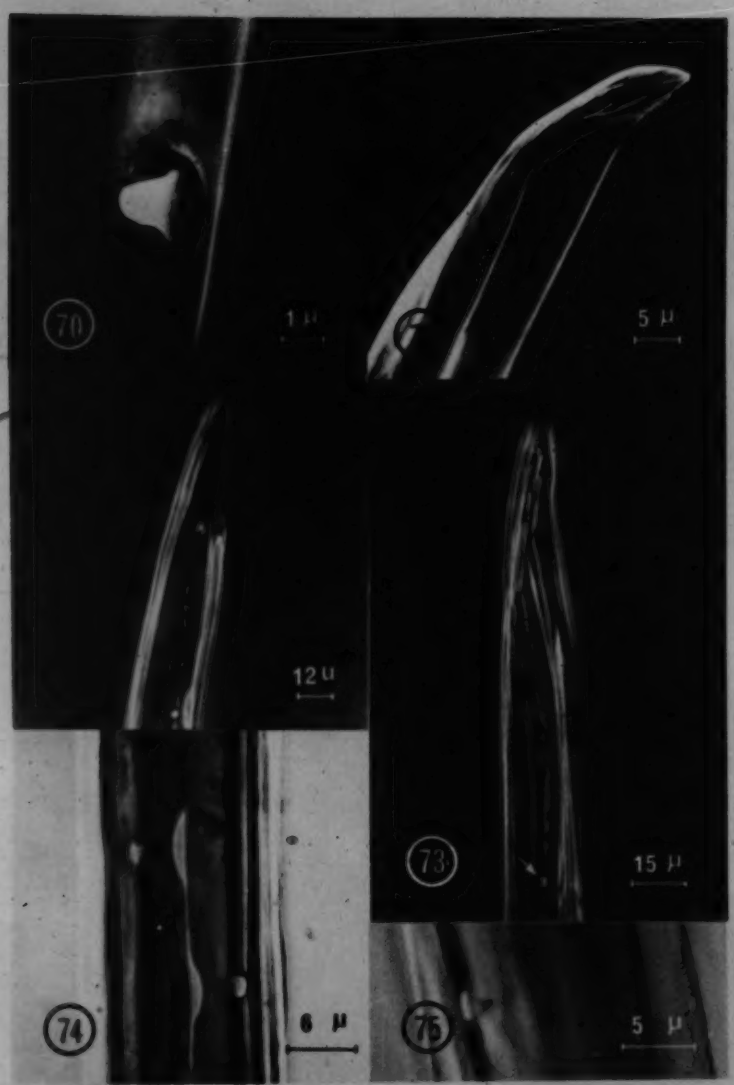


Fig. 70. Campaniform sensillum (c.s.) of female Culiseta alaskaensis.
Fig. 71. Labral tip of female Culex tritaeniorhynchus. Note the absence of c.s. in this region.
Fig. 72. Phase contrast micrograph of male Deinocerites pseudes labrum. Note the position of the c.s. (arrow).
Fig. 73. Labrum of female D.pseudes. Also note the position of the c.s. (arrow).
Fig. 74. C.s. of female Culex tritaeniorhynchus inside the food canal. Note the asymmetrical arrangement of the c.s.
Fig. 75. C.s. of male Culex erraticus.

TABLE I

Distance from the Tip of the Labrum to the Campaniform Sensilla (D), and the Relationship of this Distance to the Length (L) of the Labrum (L/D)

(No. = Number of specimens examined).

	Female			Male		
	D	L/D	No.	D	L/D	No.
Culex pipiens fatigans	153 μ	12.05	8	178 μ	10.33	4
Culex pipiens pipiens	210 μ	8.88	7	240 μ	6.96	2
Culex p. quinquefasciatus	190 μ	10.59	2	224 μ	8.65	3
Culex salinarius	199 μ	10.93	5	222 μ	10.08	6
Culex erraticus	148 μ	11.27	12	92 μ	18.89	8
Culex ocossa	150 μ	10.45	4	145 μ	11.40	8
Culex panocossa	158 μ	10.10	5	150 μ	10.98	6
Culex peccator	118 μ	12.52	8	74 μ	23.61	6
Deinocerites pseudes	142 μ	15.87	2	126 μ	20.67	2

Culex is 0.11 to 0.08 the length of the labrum from the tip, and in the males, the values vary from 0.14 in C. p. pipiens to 0.04 in C. peccator. The measurement of the distance between the c.s. and the tip of the labrum is accurate in most cases, but the length of the labrum in some preparations were approximated, as the labra were often twisted or curved in the preparations. Therefore the L/D values can be considered only as rough estimates.

In Deinocerites pseudes, the distance from the tip of the labrum to the c.s. is about 0.05 the length of the labrum in the male, and it is 0.06 in the female (Table 1).

In my 1974 study of Aedes aegypti, I proposed that the c.s. on the labrum might function as flow receptors, as these sensilla are present in both sexes of mosquitoes. Chapman et al. (1973) concluded from their experiments on the campaniform sensilla found on the legs of cockroach that indenting the dome (cap-membrane), which compresses the sensory process longitudinally, is an extremely effective experimental stimulus, rather than to stretch, pinch, or to bend it. In the mosquito labrum, the cap-membrane of many campaniform sensilla are directed anteriorly (Figs. 52, 60), so the oncoming food probably may push the cap-membrane in the direction of the socket, thus stimulating the sense organ.

The shape of the cap-membrane is also conical in the c.s. on the labrum of the larval simuliids (Craig, 1974), but peg-like in adult chaoborid Chaoborus americanus (personal observation).

2.1.1.5 Discussion

Toxorhynchites species do not feed on blood (Muspratt, 1952). Labral sense organs are totally absent in the two species studied here,

and only c.s. are present in T. splendens (von Gernet and Buerger, 1966). Male mosquitoes are never known to feed on blood in nature, although in the laboratory, they can be induced to feed on blood (MacGregor, 1931; Day, 1954; Salama, 1966; Jones and Pilitt, 1973), however, males still prefer sugar solutions to blood (Jones and Pilitt, 1973). Only c.s. are present on the labrum of the male mosquitoes examined. It appears there is a direct correlation between the presence of apical and subapical sensilla and the blood sucking habits of mosquitoes.

The retention of the apical and subapical sensilla in Wyeomyia smithii, Opifex fuscus and autogenous Aedes atropalpus is probably indicative that autogeny in these species is a recent development, if one considers blood-feeding behaviour in Diptera to be the primitive trait, as suggested by Downes (1958). With the scarcity of blood sources and in adverse weather conditions, some Arctic mosquitoes are capable of becoming facultatively autogenous (Corbet, 1967). Autogenous mosquitoes have been reported in many different genera (see Clements, 1963), and the records of these are still increasing. Spielman (1971) has reviewed the bionomics of autogenous mosquitoes, and pointed out that autogenous species are not as rare as most people believe. Nevertheless, the presence of apical and subapical sensilla in blood-sucking mosquitoes seems to indicate that these sensilla function in blood detection during probing in the host tissues, as these are the only probable chemoreceptors present in the fascicle that enters the host tissue.

Pearson (1970) using electrophysiological recording techniques, failed to get any response when the labral sense organs of female Aedes aegypti were stimulated with different chemicals. In my present study, I found the opening of the subapical sensilla in some preparations was

often occluded by a tiny peg, which was probably formed by a substance secreted by the sensillum. Stürckow (1967) found in blowflies that chemosensory hairs with their tips covered with a viscous substance were not responsive to sugar. She therefore suggested that the presence of this substance on the pore inhibits the detection of sucrose. In A. aegypti, I have reported in my 1974 study that the subapical sensilla opens through a protuberance. But my subsequent investigation reported here has indicated that the protuberance was the result of the secretion from the sensillum, and the opening is through a tiny depression on the sensillum. Therefore, if behavioural or electrophysiological studies are to be done on these labral sense organs, care has to be taken to make sure the opening of the sensilla is not occluded. It is possible that during the initial insertion of the labrum into the host tissue, any substance on the opening will be rubbed off by friction, exposing the receptive site, so the sensilla then may become responsive during probing in the host tissues. At rest, the presence of this substance on the opening might help to conserve the fluid at the receptive site.

2.1.2. Microsculpture on the dorsal wall of the labrum

On the dorsal wall of the labrum of male Aedes aegypti, I have reported a longitudinal groove extending from near the tip throughout the whole length of the labrum (Lee, 1974). Such longitudinal grooves are found in most species examined here (Figs. 76, 77), but are absent in Anopheles species, Trichoprosopon digitatum, Wyeomyia smithii, Uranotaenia lowii, and Opifex fuscus (Figs, 78, 79).

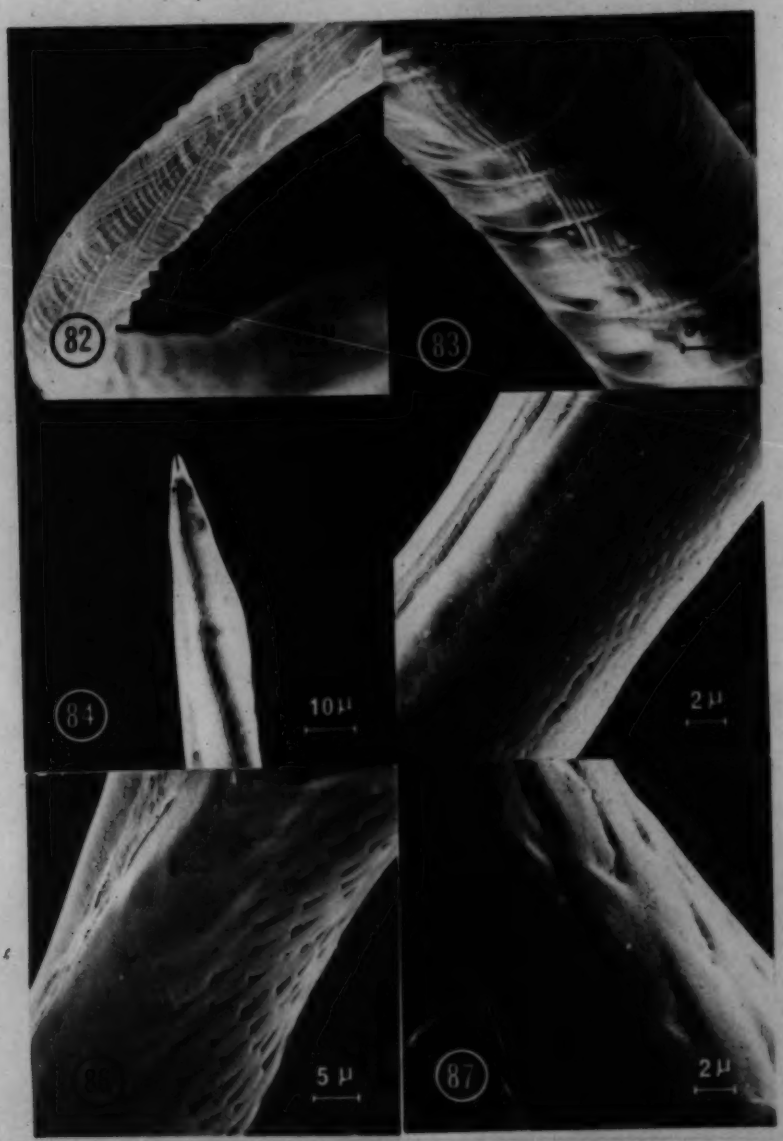
In female A. aegypti, I have also reported quadrangular cuticular thickenings on the dorsal wall of the labrum. Such microsculpture is

Figs. 76-81. Dorsal aspect of the labrum.
Fig. 76. Male Psorophora varipes. Note the dorsal longitudinal groove (arrow).
Fig. 77. Male Culex tritaeniorhynchus.
Fig. 78. Male Anopheles albimanus. Note the absence of a longitudinal groove.
Fig. 79. Male Culex erraticus. Note the forked tip of the labrum.
Fig. 80. Microsculpture on the dorsal wall of female Anopheles albimanus labrum.
Fig. 81. Same of female Anopheles stephensi.

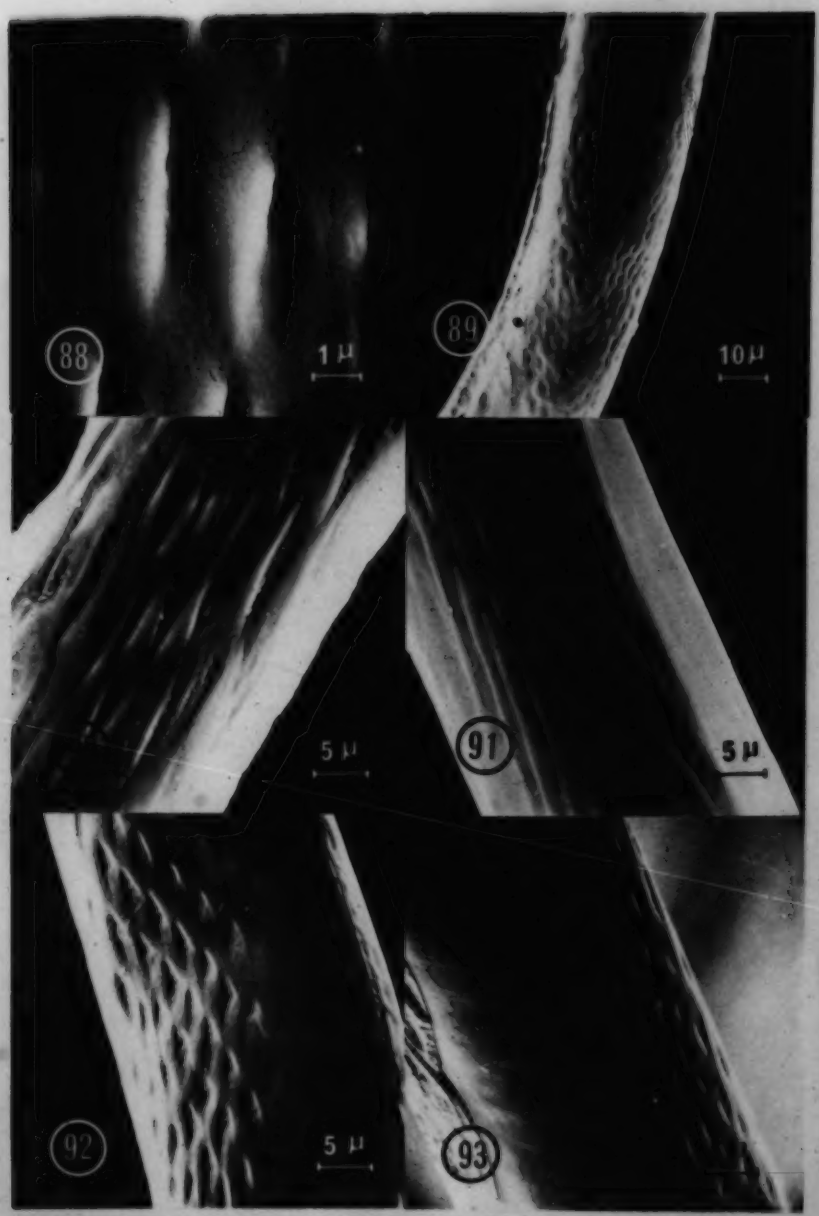
found in many species I have examined, and its structure varies among species.

In Anopheles albimanus, the dorsal wall of the labrum is almost smooth except for shallow depressions (Fig. 80), whereas in A. stephensi, the depressions are much bigger (Fig. 81). In both sexes of Toxorhynchites rutilus, the dorsal wall of the labrum has a median longitudinal groove near the tip. But proximal to the tip, an elaborate pattern consisting of oblique, longitudinal and transverse folds is found (Fig. 82). Near the middle of the labrum, this pattern changes into fine longitudinal folds and large transverse ridges (Fig. 83). In Toxorhynchites brevipalpis, the median longitudinal groove is present in both sexes (Figs. 42, 43), but whether they have such microsculpture as in T. rutilus remains to be determined. Labral microsculpture appears to be absent in Wyeomyia smithii, Coquillettidia perturbans, Opifex fuscus Culex molestus and C. declarator (Fig. 84).

Small depressions are found on the labrum of Uranotaenia lowii (Fig. 85), and the microsculpture on the labra of Orthopodomyia signifera and Eretmapodites chrysogaster is the form of V-shaped depressions (Figs. 86, 87). In Psorophora varipes, a tiny dome resembling a campaniform sensillum is found inside each cuticular depression (Fig. 88). The microsculpture in Aedes species differs from species to species. The depressions are circular in A. canadensis (Fig. 89); longitudinal with tiny domes in A. communis, A. dorsalis, A. pionips (Fig. 90); longitudinal in A. spencerii, A. togii, and A. atropalpus (Fig. 91); and triangular in A. vexans and A. cinereus (Fig. 92). The microsculpture in Armigeres durhami is similar to Aedes cinereus (Fig. 93), and that of Culiseta inornata and Deinocerites pseudes is similar to Aedes atropalpus (Fig. 94).



Figs. 82-87. Microsculpture on the dorsal wall of the labrum.
Fig. 82. Male Toxorhynchites rutilus near the labral tip.
Fig. 83. Same as above. Near the middle of the labrum.
Fig. 84. Female Wyeomyia smithii. Note the absence of microsculpture.
Fig. 85. Female Uranotaenia lowii.
Fig. 86. Female Orthopodomyia signifera.
Fig. 87. Female Eretmapodites chrysogaster.



Figs. 88-93. Microsculpture on the dorsal wall of female labrum.
Fig. 88. Psorophora varipes.
Fig. 89. Aedes canadensis.
Fig. 90. Aedes communis.
Fig. 91. Aedes atropalpus (autogenous).
Fig. 92. Aedes cinereus.
Fig. 93. Armigeres durhami.

The significance of the labral microsculpture is unknown. In the wing bases of Lepidoptera, Sharplin (1963) reported bending cuticle with characteristic cuticular depressions. Davies (1974) also found a striated band of elastic cuticle at the base of the filtering fan in larval simuliids. In both cases, the cuticle is flexible, and in blackfly larvae, the distortion of the striated cuticle generates a force which is involved in rapid fan movements (Davies, 1974). In mosquitoes, the labrum is also very flexible, and is capable of movement in various directions (Gordon and Lumsden, 1939; Griffiths and Gordon, 1952). The labrum always stains red with Mallory's Trichrome, suggesting the presence of the rubber-like protein, resilin (Weis-Fogh, 1960). It is possible the cuticular depressions on the dorsal wall of the labrum are similar to those seen on the bending cuticle reported by Sharplin and Davies.

Many workers (Christophers, 1960; Waldbauer, 1962; Hudson, 1970) have reported that the two walls of the labrum are joined laterally by the membranous lateral walls. But in female A. aegypti, I found that the membranous lateral walls are not joined to the labral nerve canal, but curled up on the latter (Lee, 1974). In the mosquitoes I have examined in this study, the membranous lateral walls of the labrum can be seen hanging loosely over the lateral side of the inner (hypopharyngeal) wall of the labrum in many species (Fig. 95).

2.2. Mandibles

These stylets are greatly reduced in or absent from most male mosquitoes. Studies on male mandibles to date are few. Mandibles are reported to be absent from male Anopheles maculipennis (Nuttall and Shipley,

Fig. 94. Microsculpture on the dorsal wall of female Culiseta inornata labrum.
Fig. 95. Ventro-lateral aspect of female Toxorhynchites rutilus labrum. Note the lateral wall of the labrum is not attached to the ventral wall.
Figs. 96-99. Mandible of female mosquitoes.
Fig. 96. Anopheles stephensi. Note the mandibular teeth.
Fig. 97. Anopheles farauti. Also note the mandibular teeth.
Fig. 98. Aedes pionips. Note the absence of mandibular teeth. Teeth seen at the bottom belong to a lacinia.
Fig. 99. Aedes togoi. Note the scalloped edges of the mandible.

1901), and in Anopheles punctipennis, Aedes stimulans and Culex pipiens (Thompson, 1905). Vizzi (1953) reported that the tip of male Anopheles quadrimaculatus mandibles are blunt. The only major study was by Marshall and Staley (1935), who examined the maxillae and mandibles of 14 species of male mosquitoes representing five genera. They found that the mandibles are present in Anopheles, Orthopodomyia, Culiseta (Culicella), and Culex (Culex) species, but are absent in Aedes (Aedes) and A. (Ochlerotatus) species.

In female mosquitoes, the mandibles are long and leaf-like, and are situated directly below the labrum. I have examined the mandibles of ten species of female mosquitoes belonging to five genera (see Appendix A).

Teeth are found on the mandibles of female Anopheles stephensi and A. farauti. The teeth in A. stephensi are approximately 1.25 μ long, 30-35 in number, and are found along the lateral edge of the mandibles (Fig. 96). They are 0.8 to 1 μ apart from each other, and point slightly posteriorly. In A. farauti, the teeth are 0.7 to 1 μ long, about 35 in number, approximately 2.2 μ apart from each other, and are also posteriorly directed (Fig. 97).

The presence of mandibular teeth in mosquitoes was reported only in Anopheles maculipennis, where Nuttall and Shipley (1901) found 31 teeth, Vogel (1921) showed 34, and Robinson (1939) reported 35-40 teeth spaced at about 2.5 μ . According to Vizzi (1953), mandibular teeth are absent in male Anopheles quadrimaculatus.

Mandibular teeth are absent in Aedes species, Culiseta inornata and Culex declarator (Figs. 98, 100). In Aedes togoi, the lateral edges of the mandibles are scalloped (Fig. 99). These scallops are probably

Fig. 100. Female Culex declarator mandible.
Fig. 101. Same of female Armigeres durhami. Note the teeth.
Figs. 102-105. Hypopharynx of female mosquitoes.
Fig. 102. Aedes communis.
Fig. 103. Aedes vexans. Note the dried saliva near the tip.
Fig. 104. Armigeres durhami.
Fig. 105. Culiseta inornata.

similar to the ones described by Waldbauer (1962) in female Psorophora ciliata. Vogel (1921) reported that mandibular teeth are absent in Culiseta annulata (reported as Culex annulata) and Culex pipiens.

In female Armigeres durhami, small, anteriorly directed teeth are found on the lateral edge near the tip of the mandibles (Fig. 101). To my knowledge, this is the first report of mandibular teeth in mosquitoes other than Anopheles species.

Robinson (1939) suggested that the mandibles in female mosquitoes cover the opening of the labrum when the latter is not in use, and protect the labrum during penetration. Later workers (Snodgrass, 1959; Christophers, 1960; Waldbauer, 1962; Hudson, 1970) agree with him about the function of the mandibles. But in female Aedes aegypti, I found that the mandibles are overlapped near the tip of the labrum, and form the floor of the labral food canal. The mandibles also serve to separate the food canal from the hypopharynx, thus forming a two-channel system: one for sucking blood, and one for injecting the saliva (Lee, 1974).

I have since found similar arrangement of the mandibles in Aedes vexans. It is very likely that mandibles in other mosquito species serve a similar function as in Aedes aegypti. Overlapping arrangement of the mandibles can be seen in the transverse sections of Culex pipiens and Anopheles mosquitoes (Vogel, 1921), and also in Culiseta inornata (Larsen and Owen, 1971). Such arrangement of the mandibles occur also in other members of Diptera. In some cases, the mandibles have an interlocking device which may also fasten them to other stylets (see Matsuda, 1965).

2.3. Hypopharynx

The hypopharynx, like the labrum, is an unpaired stylet. It is situated below the mandibles. Previous workers have considered that the hypopharynx forms the floor of the labral food canal. However, in female Aedes aegypti, I found that at the distal end of the fascicle, the mandibles form the floor of the food canal. It is only near the proximal end of the fascicle where the two mandibles spread apart, that the hypopharynx forms the food canal floor (Lee, 1974). MacGregor (1931) reported that after the removal of the hypopharynx in A. aegypti, the mosquito was still capable of drawing fluid up the food canal. Vogel (1921) and Robinson (1939) also found that the hypopharynx is not essential in the formation of the food canal.

In the present study, I have examined the hypopharynx of 26 species of female mosquitoes belonging to 11 genera using the SEM (see Appendix A). The general appearance of the hypopharynx is similar in all the species examined. It is a flat, delicate stylet, with the salivary duct located along its midline forming a ventral midrib, as in female A. aegypti (Lee, 1974).

About 8 - 10 hair-like, interdigitating cuticular projections are found at the tip of the hypopharynx (Figs. 102-106). Such hair-like projections have also been reported in female Aedes stimulans, Wyeomyia smithii and Aedes atropalpus (Hudson, 1970). A longitudinal groove on the dorsal wall of the salivary duct is found in all the specimens examined (Figs. 102-107), suggesting that the dorsal wall of the salivary duct may be interdigitated as in A. aegypti, as reported by Nehman (1968) and Lee (1974), and the salivary "duct" is in fact a groove! Therefore I think the term "salivary canal" will be more appropriate.

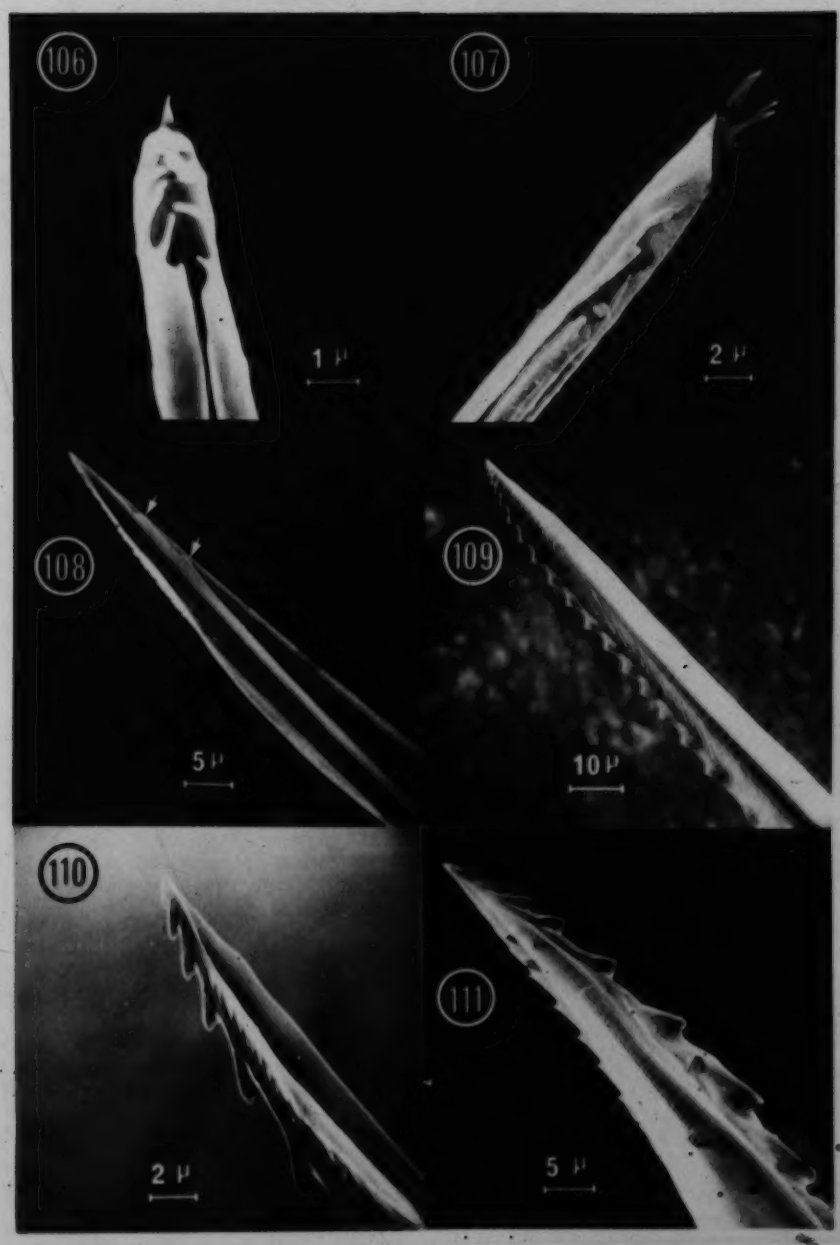


Fig. 106. Hypopharynx of female Culex tritaeniorhynchus.
Fig. 107. Same of female Toxorhynchites rutilus.
Figs.108-111. Lacinia of female mosquitoes,
Fig. 108. Anopheles farauti, showing mesial teeth (arrows).
Fig. 109. Same as above, showing lateral teeth.
Fig. 110. Anopheles stephensi. Note the absence of mesial teeth.
Fig. 111. Orthopodomyia signifera.

In Toxorhynchites rutilus, the hypopharynx in the female has only four cuticular projections (Fig. 107). About 8 - 10 cuticular projections are found at the tip of the hypopharynx in Opifex fuscus.

The salivary secretion is a thick, viscous fluid, and very often, the tip of the hypopharynx is occluded by dried saliva (Fig. 103). In my study of Aedes aegypti, I have suggested that the so-called "fascicular fluid" is the saliva, which comes out through the longitudinal interdigitated dorsal wall of the salivary canal and holds the stylets together (Lee, 1974).

I have also suggested in the same study that the finger-like projections at the tip of the hypopharynx might help to conserve saliva when the mosquito is feeding on sugar solutions. But my later investigation reported here of the hypopharynx in other species shows that the finger-like processes in many species are not big enough to close the apical salivary canal opening (Figs. 102, 105, 106), indicating that these projections might serve other purposes.

During blood feeding, saliva injection is reported to precede and/or accompany the act of blood-sucking (Nuttall and Shipley, 1901; Gordon and Lumsden, 1939; Griffiths and Gordon, 1952). Dr. W. Horsfall's film on the feeding behaviour of female Aedes aegypti on the foot-web of a frog also shows the injection of saliva as little "puffs" during probing and also during withdrawal of the fascicle. Devine et al. (1965) found that A. aegypti leaves a mean of 4.7 µg of saliva in a mouse when it takes a blood meal. Orr et al. (1961) observed that salivary glands in female A. aegypti become active again 24 hours after a blood meal, probably to replenish the saliva lost during feeding. But Hudson (unpublished, from Orr et al., 1961) found that female A. aegypti deprived of

saliva are still capable of normal feeding, laying eggs which hatched, and the larvae developed successfully into adults, indicating that saliva may not be important in normal feeding. Nonetheless, the injection of saliva during probing and withdrawal of the fascicle seems to be an integral part of the feeding process. The cuticular projections at the tip of the hypopharynx may prevent possible blockage of the apical salivary canal opening by pieces of small tissue when the mosquito is probing with its fascicle inside the host tissue for a suitable feeding site.

In male mosquitoes, the hypopharynx is fused to the ligula distally, and to the labium proximally (Nuttall and Shipley, 1901; Thompson, 1905; Vogel, 1921; Marshall and Staley, 1935; Vizzi, 1953; Christophers, 1960; Lee, 1974). Since the mandibles in many male mosquitoes are either greatly reduced or totally absent, the ventral closure of the food canal is formed by the hypopharynx. This kind of food canal formation probably is not as efficient as in the females. Nuttall and Shipley (1901) found that when the mosquitoes were allowed to feed on milk and sugar, the males took a longer time than the females to feed, although the males exerted themselves more in feeding.

The dorsal wall of the salivary canal in male mosquitoes also has an interdigitated opening as in the females (Lee, 1974). The salivary glands in male mosquitoes are rather small compared to females, and appear almost vestigial (Metcalf, 1945; Orr et al., 1961). Neither agglutinins nor anticoagulins are found in the salivary glands of male Anopheles quadrimaculatus (Metcalf, 1945). Agglutinins and anticoagulants are found in the saliva of some female mosquitoes (see Gooding, 1972 for review), but many species still feed successfully without these substances

(e.g. Aedes aegypti). As the composition of mosquito saliva is still poorly known, our knowledge on the role of the saliva in feeding is still fragmentary.

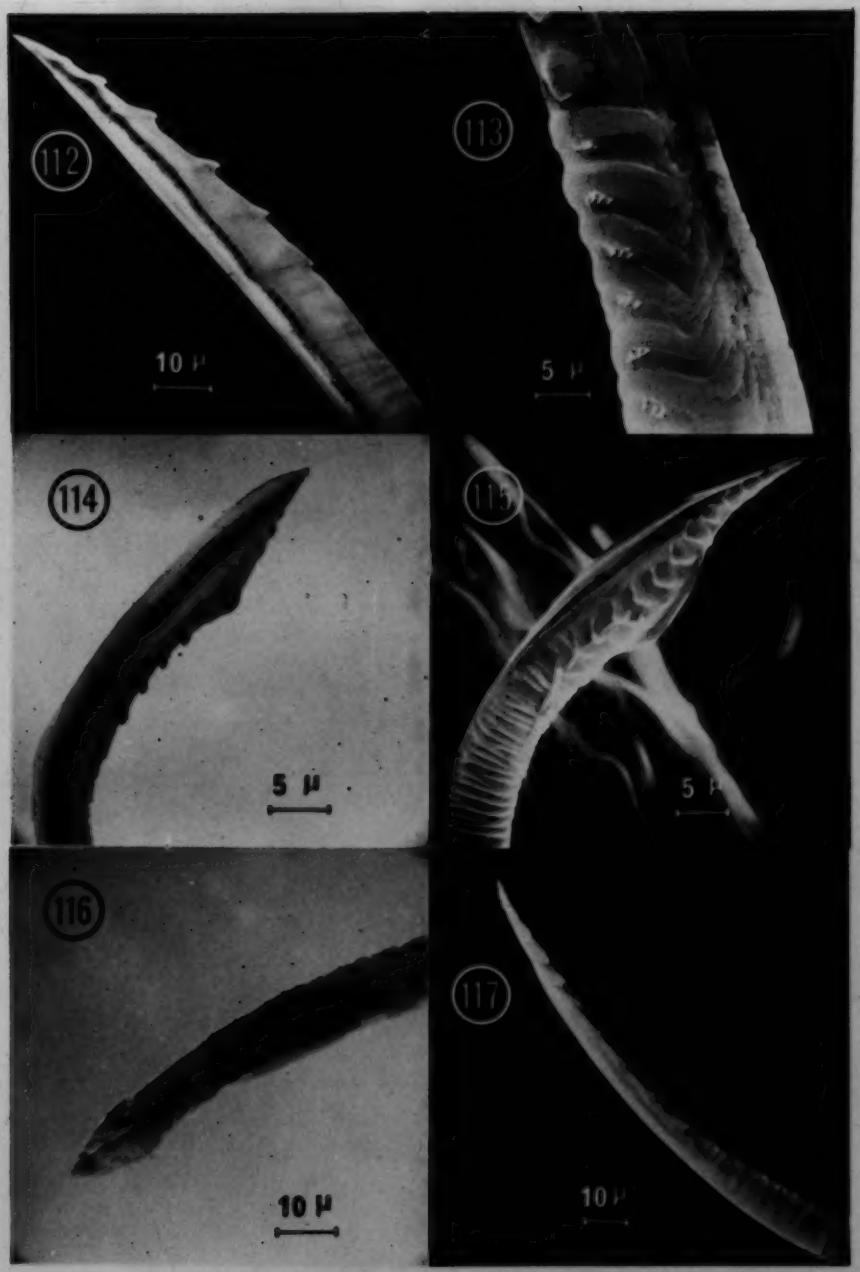
2.4. Maxilla

The two maxillary stylets of mosquitoes have long been considered to be the galea, but most recent authors have called them laciniae (Snodgrass, 1959; Matsuda, 1965; Nehman, 1968; Hudson, 1970), except for Owen et al. (1974) who labeled them as mandibles in their paper on female Culiseta inornata.

In female mosquitoes, the laciniae are situated on either side of and below the midrib of the hypopharynx. Each lacinia is thickened at its inner margin and is membranous laterally. At its distal end, the outer margin is thickened, and bears a row of proximally-directed lateral teeth (Figs. 109-115, 117, 118, 122). A row of distally-pointed mesial teeth occur also on the mesial side of the stylet (Figs. 108, 111, 118). Posterior to the lateral teeth, the lacinia is usually annulated, and bears consecutive rows of vestigial teeth in line with the lateral teeth. The vestigial teeth occur usually only in the distal one-third of the lacinia.

Although the laciniae are also present in male mosquitoes, they are usually reduced compared to females (Marshall and Staley, 1935). In Aedes aegypti, teeth and annulations are absent on the male stylets (Lee, 1974).

Robinson (1939) has pointed out the importance of the laciniae in penetrating host tissues, and found that mosquitoes with both



Figs. 112-117. Lacinia of female mosquitoes.
Fig. 112. Culiseta morsitans.
Fig. 113. Trichoprosopon digitatum.
Fig. 114. Uranotaenia lowii.
Fig. 115. Culex territans.
Fig. 116. Toxorhynchites rutilus.
Fig. 117. Opifex fuscus.

Figs. 118-123. Lacinia of female mosquitoes.
Fig. 118. Culiseta inornata.
Fig. 119. Deinocerites pseudes. Note the absence of vestigial teeth.
Fig. 120. Aedes atropalpus (autogenous). Note the comb-like vestigial teeth arranged in a row behind the lateral teeth.
Fig. 121. Culiseta inornata. Note the vestigial teeth are arranged in patches.
Fig. 122. Same as above. The posterior edge of some lateral teeth is fringed with vestigial teeth.
Fig. 123. Aedes atropalpus (autogenous), showing three hairs near the base of the lacinia.

laciniae cut off could not be induced to feed, though mosquitoes with only one lacinia could still feed, but with great difficulty. He has also given a detailed description of the mechanism of piercing by the laciniae during feeding.

Roubaud (1928) suggested that differences in the average number of teeth on a single lacinia (maxillary index) in individuals of Anopheles maculipennis from various geographical regions of the world can be related to the differences in the thickness of the skin of their respective host (cited from Robinson, 1939). However, Robinson (1939) argued that since mosquitoes with only one lacinia left can still feed successfully on a host, the addition or substraction of a tooth from the stylet will not make any difference on the type of the hosts.

The main purpose of the present study on the laciniae was to determine if the number of maxillary teeth in different species of mosquitoes can be related to their hosts. The laciniae of 31 species of female mosquitoes belonging to 14 genera were examined using SEM. For each species, at least three specimens were examined. The number of teeth and the number of specimens studied were listed in Table II. The lateral teeth are usually very easy to see using LM. But to see the mesial teeth, SEM is necessary, as these teeth are rather thin and small, and very often, the specimens have to be rotated in order to get the right angle to observe them.

In the following description, most of the information regarding the hosts of the mosquitoes came from Horsfall (1955); Carpenter and LaCasse (1955); Gillett (1971); and Wright and DeFoliart (1970), unless otherwise stated.

TABLE II

Table Showing the Number of Lateral (Lt) and Mesial (Mt) Teeth; the Presence (+) or Absence (-) of the Vestigial Teeth (Vt), and the Hosts of the Mosquitoes studied.

Species	Lt	Mt	Vt	Hosts
Anopheles farauti	18 or 19	2		WB
Anopheles stephensi	13	None		WB
Anopheles merus	14	None		WB
Toxorhynchites rutilus	None	None		NB
Trichoprosopon digitatum	12	None	+	A
Coquillettidia perturbans	12	None	-	WB
Uranotaenia lowii	15	None		CB
Orthopodomyia signifera	16	5		A
Psorophora ferox	21 or 22	6 - 8		WB
Psorophora varipes	21 or 22	5, 6		BS
Eretmapodites chrysogaster	16	3, 4		man
Aedes communis	17	5	+	man
Aedes excrucians	15	3 - 5		man
Aedes fitchii	21	5 - 7		WB
Aedes flavescens	14	4		WB
Aedes atropalpus (autogenous)	14	4	+	NB
Aedes togoi	11	5		BS
Aedes polynesiensis	11	5		BS

TABLE II (Continued)

Species	Lt	Mt	Vt	Hosts
Aedes vexans	23	4		WB
Aedes cinereus	16	7		WB
Armigeres durhami	16	5		BS
Armigeres subalbatus	14	5		BS
Opifex fuscus	12	4	+	NB
Culiseta alaskaensis	11	5		man
Culiseta inornata	14	4	+	WB
Culiseta morsitans	8	None	+	A*
Culex territans	15	None	-	CB
Culex pipiens molestus	12 or 13	None	-	man
Culex tritaeniorhynchus	12 or 13	None	-	A, pigs*
Culex salinarius	12	None	-	BS
Deinocerites pseudes	13	4	-	WB

A = birds

BS = blood-sucking

CB = cold-blooded animals

WB = mammals

NB = non-blood sucking

* = host identity still doubtful

2.4.1. Lateral and Mesial Teeth

Both Anopheles farauti and A. merus feed on man and other animals and are vectors of malaria, with A. farauti being important in the transmission of filariasis (Bryan, personal communication). The number of lateral teeth is quite different in these species (Table II). Mesial teeth are found only in A. farauti (Fig. 108). Oblique striations are found beside the lateral teeth in the three anopheline species studied (Figs. 109, 110).

Mosquitoes that are primarily bird feeders are Trichoprosopon digitatum (Davis, 1944, from Horsfall, 1955), Orthopodomyia signifera (H. C. Chapman, personal communication), Culiseta morsitans and Culex tritaeniorhynchus. Mesial teeth are absent in all of them except O. signifera (Table II), which has five mesial teeth (Fig. 111). The number of lateral teeth ranges from 8 in C. morsitans (Fig. 112) to 16 in O. signifera. In T. digitatum, using the LM, the number of lateral teeth appears to be 16-18, but only 12 are seen with SEM. This is because the annulations following the lateral teeth are so thickened (Fig. 113) that they appeared as "teeth" under the LM. Therefore if one is to use LM to count the number of maxillary teeth, caution has to be taken not to count the annulations as teeth!

Mosquitoes that feed on cold-blooded animals like frogs and toads are Uranotaenia lowii (Remington, 1945; H. C. Chapman, personal communication) and Culex territans. Mesial teeth are absent in both species, and the number of lateral teeth is 15 in both species (Figs. 114, 115). Here, as in bird feeding species, the absence of mesial teeth seems to be related to the host. But mesial teeth are also absent in some mosquitoes that feed on man and other mammals (Table II).

In Toxorhynchites rutilus where the adults feed only on plant nectar (Muspratt, 1952), both lateral and mesial teeth are absent (Fig. 116). But in Opifex fuscus where the adults are never known to feed on blood (Horsfall, 1955: D. A. Craig, personal communication), both lateral and mesial teeth are present (Fig. 117). The adults of Wyeomyia smithii are also not known to feed on blood (Price 1958), and Hudson (1970) found 8 - 10 lateral teeth in the females of this species. She also found 14 lateral and 4 mesial teeth in the autogenous and anautogenous forms of Aedes atropalpus. I found the same number of teeth in the autogenous strain of this mosquito I obtained from Dr. R. Brust of the University of Manitoba.

The rest of the mosquitoes listed in Table II not mentioned above all feed on man and other mammals, including Armigeres subalbatus (Dao Van Ty, 1945, cited from Baar, 1964) and Armigeres durhami (Cheong and Omar, 1967). Both lateral and mesial teeth are present in these species (Table II).

The number of maxillary teeth is variable even within the same species, as noted by Kulagin (1905). In Anopheles maculipennis, Nuttall and Shipley (1901) found 13 lateral teeth, but Vogel (1921) reported 16. In Culiseta annulata, Vogel (1921, reported as Culex annulata) found 14, but Schiemenz (1957, reported as Theobaldia annulata) found 9 - 12 lateral teeth. In A. aegypti, the number of lateral teeth varies between 10 and 12 (Lee, 1974).

It is clear from the data presented above, that there is no obvious relation between the number of lateral teeth, or the presence or absence of mesial teeth, to the type of hosts that the mosquites feed on.

The lateral teeth are important in piercing and withdrawal of the fascicle during feeding, as described by Robinson (1939). The function

of the mesial teeth is still uncertain. In female A. aegypti which have been blood-fed once, the sharp points on the mesial teeth show no visible damage. In some species, the mesial teeth are without sharp points (Figs. 108, 117, 118). The fact that the mesial teeth are absent in many blood-sucking mosquitoes probably indicates that they do not play a vital role in feeding.

2.4.2. Vestigial Teeth

Posterior to the lateral teeth, and in line with these are consecutive rows of vestigial teeth. Such vestigial teeth have been reported by Hudson (1970) in Aedes stimulans, Aedes atropalpus and Wyeomyia smithii, and in Aedes aegypti by Lee (1974).

Vestigial teeth are absent in Culex and Deinocerites species examined (Figs. 115, 119). In those mosquitoes with vestigial teeth, three different patterns were found depending on the species. In Aedes atropalpus (autogenous) and Opifex fuscus, the vestigial teeth are in linear comb-like groups (Fig. 120), as in female A. aegypti reported by Lee (1974). In Aedes communis, Culiseta inornata and Culiseta morsitans, the vestigial teeth are in circular patches (Fig. 121). Vestigial teeth in Trichoprosopon digitatum are arranged in horizontal rows of 3 to 4 near the anterior end of the lacinia on the annulations (Fig. 113), with the last few rows having only 2 teeth. In Culiseta inornata, the proximal edges of the posterior lateral teeth are also fringed with vestigial teeth (Fig. 122).

In all the species examined in this study, the vestigial teeth occur only at the distal end of the lacinia. Near the base of the lacinia in Aedes atropalpus, three little hairs which point posteriorly are found (Fig. 123). The significance of these hairs is unknown.

2.5. Inability of Newly Emerged Female Mosquitoes to Feed

The fact that mosquitoes do not take a blood meal immediately following emergence has been noted by many workers, and Christophers (1960) has already reviewed this subject. However, very few explanations for such behaviour were given. Jones and Pilitt (1973) found that majority of female Aedes aegypti took their first blood meal when they were 23 to 26 hours old, and they attributed this behaviour to activation by a hormone, but presented no evidence to support it.

Nuttall and Shipley (1901) suggested that newly hatched mosquitoes are unable to perforate the skin of the host until the mouthparts have hardened, a process requiring a variable length of time. In Aedes aegypti, I reported that the fascicular stylets in teneral mosquitoes are not fully sclerotized immediately following emergence (Lee, 1974). Moreover, in A.aegypti less than five hours old, the labellar lobes and the labial gutter are full of cellular elements as compared to older adults (see Lee, 1974, Figs. 4, 5, 10, and 11 where 11 is that of an older adult), indicating that the development of the labium is not complete, thus supporting the suggestion of Nuttall and Shipley.

In Anopheles quadrimaculatus, Metcalf (1945) reported that the salivary glands of newly emerged adult females become fully developed 8 to 12 hours after emergence.

3. Cibarium

This is a muscular pump situated at the proximal end of the labrum, a structure often referred to as the pharynx by many workers. Snodgrass (1959) noted that this structure is homologous to the cibarium of the cockroach, and I here follow his interpretation.

The mosquito cibarium is a dorso-ventrally flattened, tubular structure lying under the clypeus. At its anterior end, the cibarium is attached to the ventral wall of the labrum dorsally, and to the dorsal surface of the hypopharynx ventrally. Posteriorly, the cibarium is connected to the pharyngeal pump. For a detailed description of the cibarium and its musculature, see Christophers (1960).

Sense organs are present inside the mosquito cibarium, as already noted by many workers (see Lee, 1974 for review). Behavioural studies have indicated that the cibarial sense organs are probably sensitive to blood and sugars (Day, 1954; Hosoi, 1959; Owen, 1963, 1965), and also to unacceptable compounds (Owen, 1963; Salama, 1966), thus suggesting an important role these sense organs might play in the feeding behaviour of the mosquitoes.

Specialized hair-like structures located in the postero-ventral wall of the cibarium are found in some Anopheles and in all Culex females examined, structures which Annett, Dutton and Elliott (1901) termed "rods and cones" (cited from Patton and Evans, 1929). Patton and Evans (1929) referred to these structures as "specialized hairs" in female Anopheles costalis. Later workers called these structures either bucco-pharyngeal or cibarial armatures, and their taxonomic importance was pointed out by Sinton and Covell (1927), Barraud and Covell (1928) and Michener (1944).

In this study, I examined the cibaria of 37 species of mosquitoes representing 10 genera with LM, and that of female Anopheles farauti, Aedes aegypti, Culiseta inornata and Culex declarator with SEM (see Appendix A). The probable functions of the cibarial sense organs and the cibarial armature are discussed on the basis of the behavioural studies of earlier workers. The taxonomic importance of the cibarial armature in mosquitoes of the Culex (Melanoconion) complex is also discussed.

In the following description, the terminology for the cibarial sense organs is the same as Lee (1974) (Fig. 124). At least four specimens were studied for each sex of each species. Unless otherwise mentioned, the following description applies to both sexes of mosquitoes.

3.1. Size of the Cibarium

The length of the cibarium was taken from the isthmus between the labrum and the anterior hard palate to the posterior edge of the cibarium between the two lateral flanges (Fig. 124). For species with cibarial armature, the length was taken up to the median posterior end of the armature.

Generally, the length of the cibarium is twice its width, and the anterior hard palate is about one-third the length of the cibarium, though there are exceptional cases. For instance, in Wyeomyia smithii and Toxorhynchites species, the anterior hard palate is about half the length of the cibarium (Figs. 126, 127). The other exception is in Psorophora species. In P. ferox, the length of the cibarium is about 4.5 times its width in the males, although in females, the length is only twice its width (Fig. 130). In P. varipes, the length of the

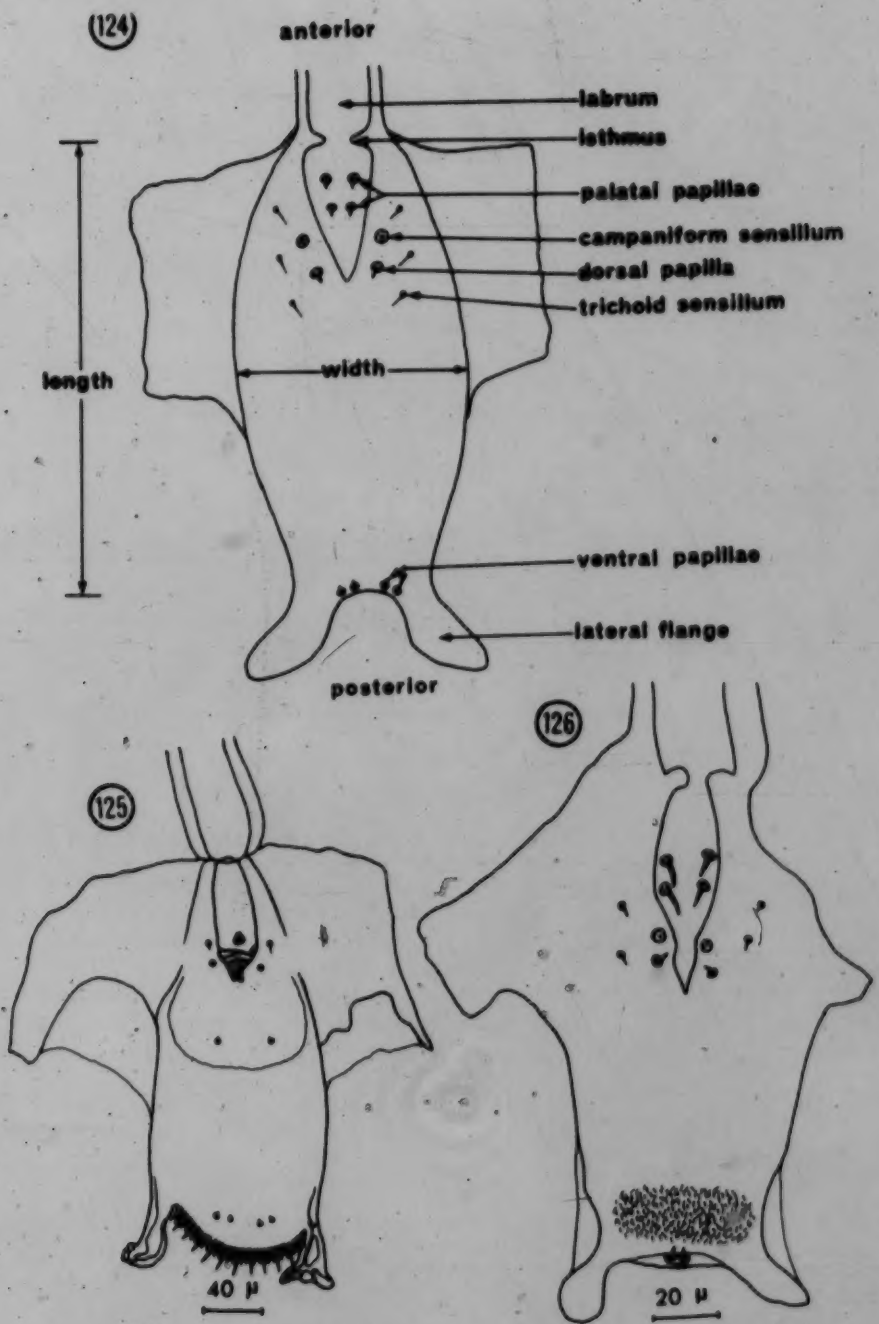
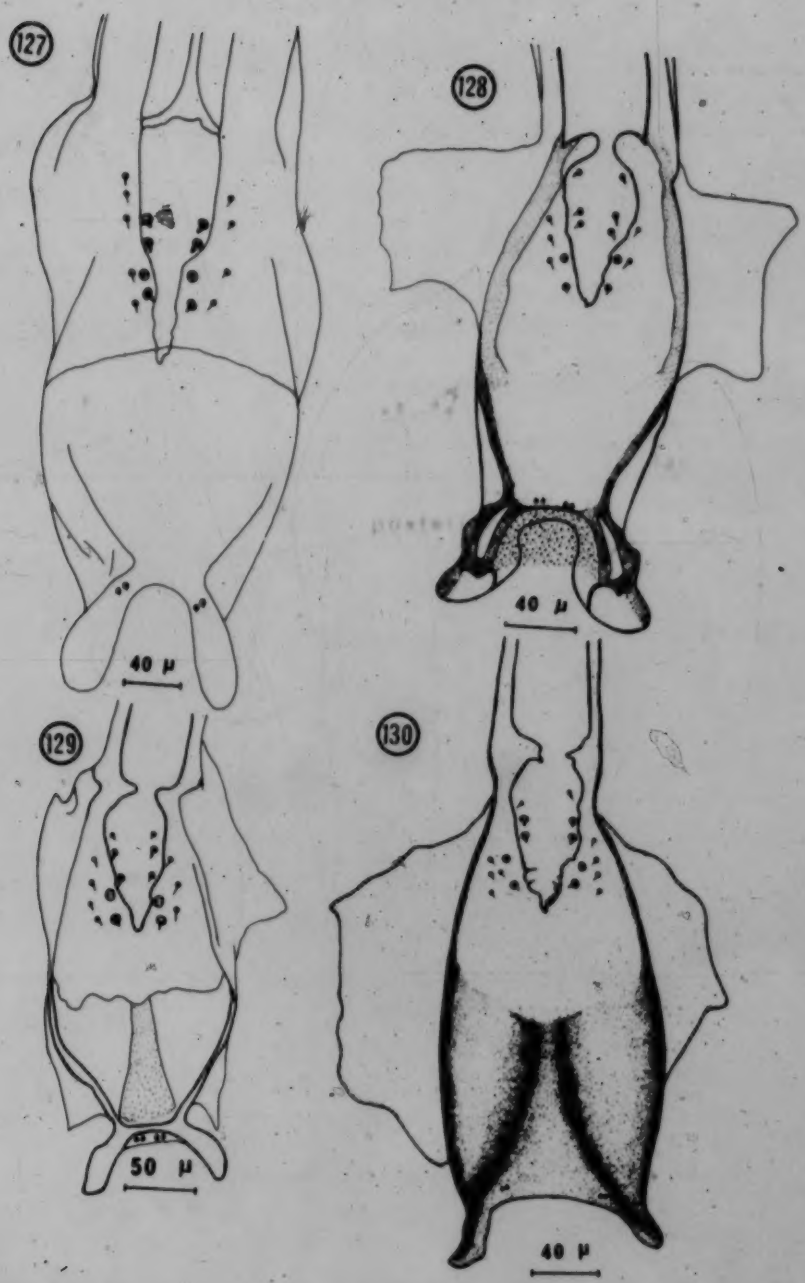


Fig. 124. Dorsal aspect of a generalized cibarium to show the position of the sense organs, and the way the measurements were taken.
Fig. 125. Cibarium of female Anopheles stephensi.
Fig. 126. Same of Wyeomyia smithii.



Figs. 127-130. Cibarium of female mosquitoes.
Fig. 127. Toxorhynchites splendens.
Fig. 128. Coquillettidia perturbans.
Fig. 129. Aedes dorsalis.
Fig. 130. Psorophora ferox.

cibarium is 3.7 times its width in the males, and 3 times in the females.

The male cibarium is always absolutely smaller than the female, due to the relative size of the adults.

3.2. Cibarial Sense Organs

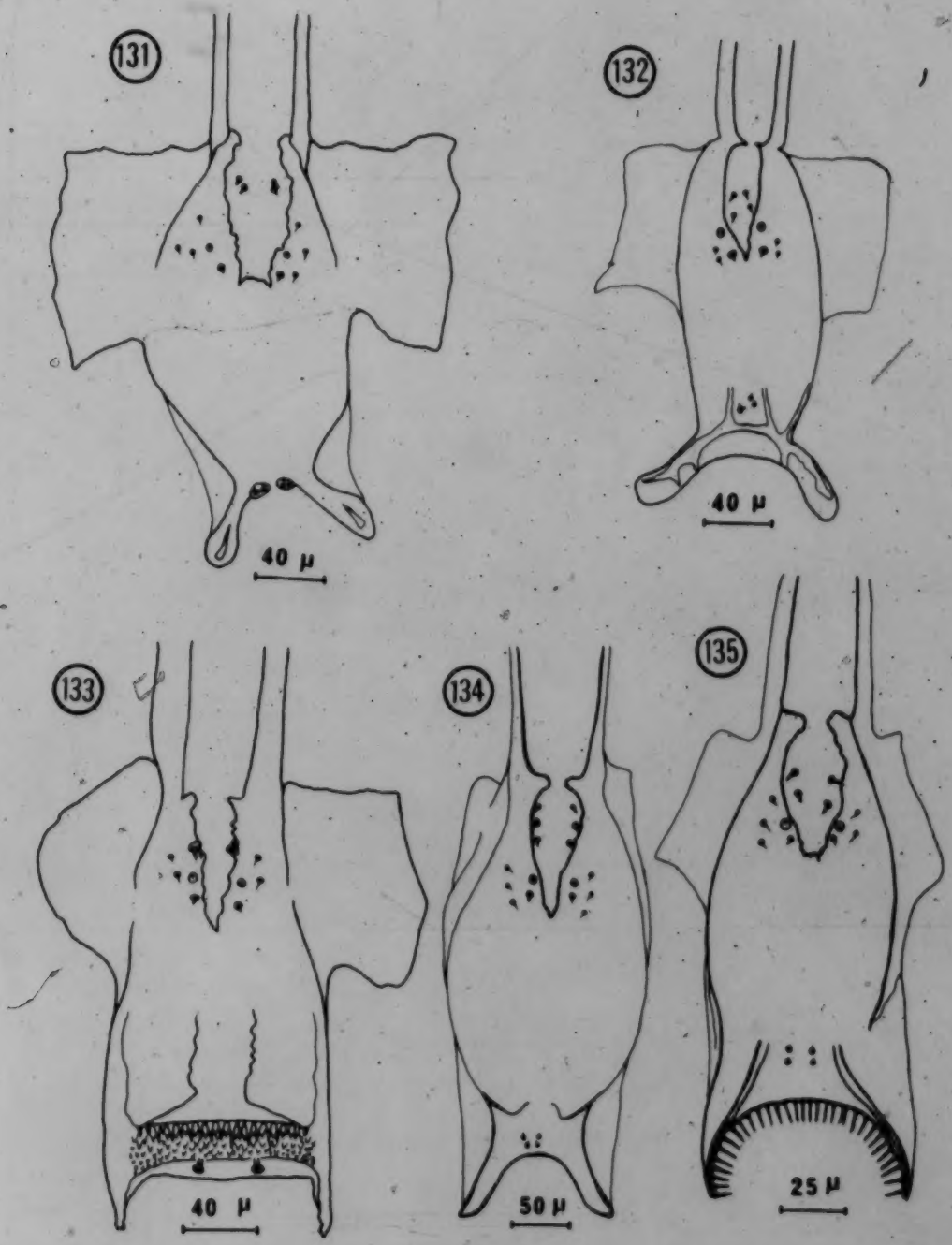
3.2.1. Palatal Papillae

These papillae are socketed at the base, and are located on the anterior dorsal hard palate (dhp) of the cibarium (Fig. 124). Sinton and Covell (1927) were probably the first to have noticed the presence of these papillae in mosquitoes, and called them palatal papillae. The number of papillae is usually four in Anopheles, Toxorhynchites, Armigeres, Culex, most Aedes and in Wyeomyia smithii and Opifex fuscus (Figs. 125-127, 131-133, 135). In Psorophora and Culiseta species, and in Aedes dorsalis and Coquillettidia perturbans, the number of the papillae is six (Figs, 128-130, 134, 138).

3.2.1.1. Mosquitoes with Four Palatal Papillae

In mosquitoes having four palatal papillae, the papillae are normally arranged in a quadrangle near the middle of the dph., but there are exceptional cases.

In Anopheles mosquitoes, the papillae have short papillar shaft and are closely packed in one group near the posterior end of the dhp. (Fig. 125). Sinton and Covell (1927) also found this arrangement in the Anopheles mosquitoes they studied. Nuttall and Shipley (1903)



Figs. 131-135. Cibarium of female mosquitoes.
Fig. 131. Aedes atropalpus (autogenous).
Fig. 132. Armigeres durhami.
Fig. 133. Opifex fuscus.
Fig. 134. Culiseta alaskaensis.
Fig. 135. Culex ocossa.

noted the palatal papillae in longitudinal sections of female Anopheles maculipennis, but regarded them as cuticular folds!

In Toxorhynchites species, the papillae are mostly arranged in a quadrangle near the middle of the dhp. (Fig. 127). However, in some individuals of T. rutilus, two papillae on one side are very closely situated, and share a single socket, thus giving the impression that the specimen has only three papillae.

Palatal papillae in Opifex fuscus are arranged in groups of two each on the lateral edge of the dhp. (Fig. 133). Arrangement of the palatal papillae is mostly quadrangular in Aedes, Armigeres and Culex species, and also in Wyeomyia smithii (Figs. 126, 131, 132, 135). But in some female Aedes communis, male Aedes togoi, and both sexes of some Culex erraticus, three palatal papillae were found on one side of dhp., with only one on the other side of the dhp. In Culex (Lutzia) fuscanus, the arrangement of the palatal papillae is different from other Culex mosquitoes in that they are closely packed in one group near the centre of the posterior half of the dhp., similar to the arrangement in Anopheles mosquitoes. Barraud and Covell (1928) have also noted this peculiarity.

More than four palatal papillae were found in some Aedes mosquitoes. In one each of female A. canadensis, and A. vexans, and in one male A. aegypti, a small papilla with a small socket was found anterior to the papillar quadrangle on one side of the dhp.

The size of the socket and the length of the papillae are variable. In Anopheles mosquitoes, the socket diameter averages 3 μ, and the papillae are 2 to 3 μ long, except in A. earlei, where the papillar length averages 4 μ in the males and 7 μ in females. In Culex fuscanus

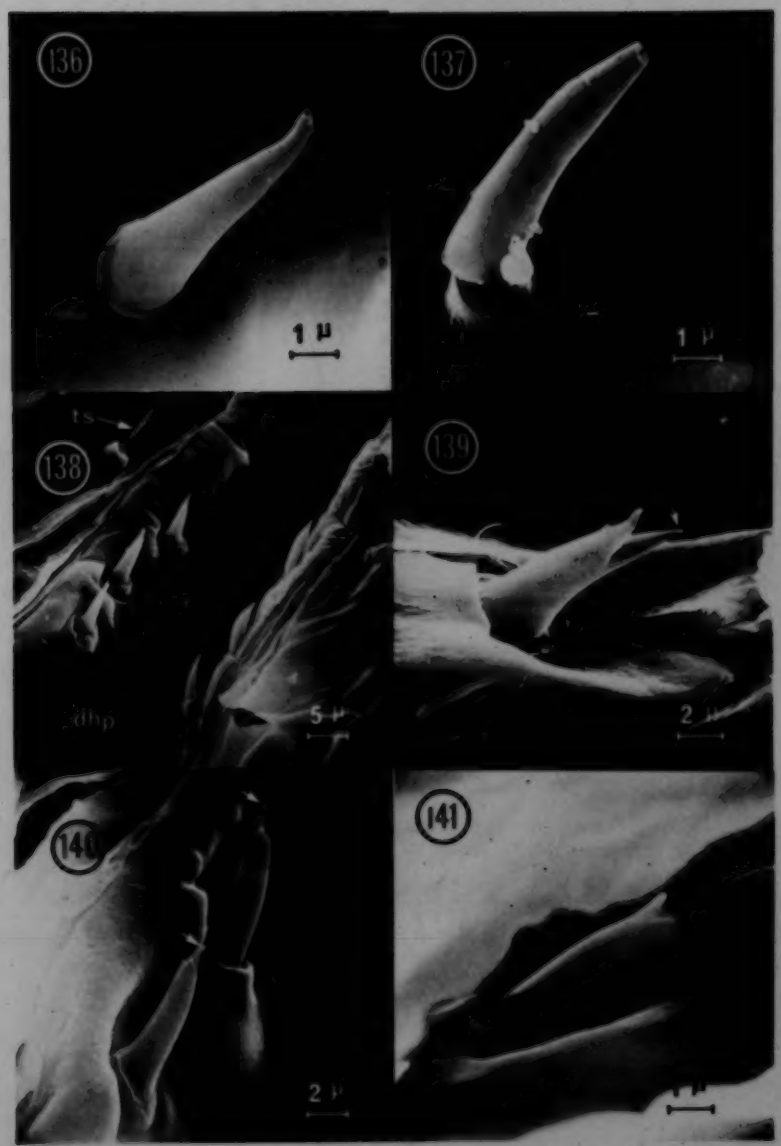
where the papillar arrangement is similar to the Anopheles mosquitoes, the socket diameter averages 3.5 μ, and the papillae are 7 - 10 μ long.

In Opifex fuscus and in Toxorhynchites species, the socket diameter averages 5 μ, and the papillae are 7 - 10 μ long, with some T. brevipalpis having the longest papillae, up to 15 μ. Socket diameter in Wyeomyia smithii and Armigeres species averages 5 μ and the papillae are 10 - 12 μ long.

In Aedes species, the socket diameter ranges from 2.5 μ in female A. atropalpus and male A. polynesiensis to 6.5 μ in female A. canadensis and A. trichurus. The length of the papillae ranges from 5 μ in male A. togoi to 10 μ in female A. trichurus. In Culex mosquitoes, the socket diameter averages 3.5 μ, and the papillae are 3 - 7 μ long.

Using the SEM, an opening 0.15 μ in diameter is found at the tip of palatal papillae in female A. aegypti (Figs. 136, 137). The socket is not as distinct as seen with LM, but the diameter of the socket is 3 μ, and the papillae are 7.5 - 10 μ long, as reported by Lee (1974). In one specimen of female Aedes communis, a palatal papilla with a bifurcated tip was observed with LM. Papillae with bifurcated tips are quite common in female Culiseta inornata (see below).

Dapples and Lea (1974) have obtained SEM pictures of some cibarial sense organs of A. aegypti using freeze-fracture method, but described them only as sensory receptors. Their Figure 2 shows two palatal papillae, Figure 3 a trichoid sensillum, and Figure 4 a campaniform sensillum.



Figs. 136-141. Cibarial sense organs of female mosquitoes.
Fig. 136 and 137. Palatal papillae of Aedes aegypti, showing the apical opening.
Fig. 138. Culiseta inornata, showing six palatal papillae on the anterior dorsal hard palate (dhp). ts, trichoid sensillum.
Fig. 139. Palatal papilla of Culiseta inornata with bifurcated tip.
Fig. 140. Arrow points to the probable opening of the papilla. Same as above, with an unknown substance at the tip of the papillae (arrows).
Fig. 141. Palatal papilla of Culiseta inornata with four-pronged tip.

3.2.1.2. Mosquitoes with Six Palatal Papillae

In mosquitoes with six palatal papillae, the papillae are usually situated on the anterior half of the dhp., and point posteriorly (Figs. 128-130, 134), except in Aedes dorsalis, where the papillae are situated near the middle of the dhp. (Fig. 129). They are normally arranged in two rows of three each on the lateral sides of the dhp. (Figs. 128 - 130, 134, 138). The most anterior pair are often situated slightly apart from the rest, and are smaller in size. The remaining four form a quadrangle as in those mosquitoes with four palatal papillae. Using LM, the socket diameter of the first pair of palatal papillae averages 2 - 3 μ, and the papillae are 5.0 - 8.5 μ long; the second and third pair have a socket diameter of 4 - 6 μ, and the papillae are 5 - 12 μ long. The socket diameter and the papillar shaft are smaller in the males than in the females.

In the cibaria of female Coquillettidia crassipes (reported as Taeniorhynchus crassipes), Culiseta (=Theobaldia) niveitaeniata, Culiseta (=Theobaldia) longiareolata and Aedes caspius (reported as Ochlerotatus caspius), Barraud and Covell (1928) also found three pairs of palatal papillae.

In female Culiseta inornata, under the SEM, the sockets of the palatal papillae are very distinct in most cases (Figs. 138 - 141). Many of the papillae have bifurcated tips (Figs. 138 - 140), and such papillae are not limited to any particular pair. The opening in these papillae appear to occur on only one of the bifurcations (Fig. 139, arrow). In some cases, a droplet is found at one of the two tips (Fig. 140, arrows). In some papillae, the tip is four-pronged (Fig. 141), with two long and two short prongs. In the simple papillae, an opening of 0.2 - 0.25 μ in

diameter is found at the tip (Fig. 142). The fact that these papillae open through the tip suggests that they might be thick-walled chemoreceptors.

Sensilla with bifid tips were reported on the prementum of the Prairie grain wireworm Ctenicera destructor by Bellamy (1973), and also on the labella of the tsetse fly Glossina austeni by Rice et al. (1973a). In the wireworm, Bellamy found that the hair is innervated by a single dendrite which appears to penetrate a short distance into a central lumen, and the tip of the dendrite contains a tubular body. In the tsetse fly, Rice et al. reported that the setiform sensilla with bifid tips (LR5) are innervated by a mechanoreceptive dendrite terminating at the base, and one chemoreceptive dendrite extending to the tip of the seta. From their electrophysiological studies, they suggested that these sensilla probably detect the NaCl and ATP.

3.2.2. Campaniform Sensilla

These are found in all the mosquitoes examined. They are situated one on either side of the posterior half of the dhp. on the dorsal membranous wall of the cibarium (Figs. 124-135).

In Culex and most Anopheles species, the average diameter of the campaniform sensilla is 3.5 μ. But in A. earlei, the diameter is 5 - 6 μ. In Toxorhynchites and Aedes species, the campaniform sensilla have a diameter of 4 - 8 μ, depending on the species. In the rest of the species listed in Appendix A but not mentioned above, the diameter of the campaniform sensilla averages 4.5 μ.

Under the SEM, the shape of the cap-membrane in the campaniform sensilla is very similar to that in the labral campaniform sensilla.

Figs. 142-147. Cibarial sense organs of female mosquitoes.
Fig. 142. Culiseta inornata, showing the apical opening of one palatal papilla.
Fig. 143. Campaniform sensillum of Culiseta inornata.
Fig. 144. Palatal papillae (pp), trichoid sensillum (ts), and campaniform sensillum (cs) of Aedes aegypti.
Fig. 145. Trichoid sensillum (ts) and a dorsal papilla with bifid tip in female Culiseta inornata. Arrow points to the probable site of the opening.
Fig. 146. Ventral papillae (vp) of Anopheles farauti. Note the cibarial armature posterior to these papillae.
Fig. 147. Same as above, showing the apical opening of the ventral papilla.

In Aedes aegypti, the cap-membrane is usually conical, like that in female Culiseta inornata (Fig. 143). But in some cases, the apex of the cap-membrane is notched (Fig. 144), as in the labral campaniform sensilla of some mosquitoes (Fig. 65).

In the cibarium of the blowfly Callíphora erythrocephala, Rice (1973) found four campaniform sensilla, but the shape of the cap-membrane is dome-shaped.

Sinton and Covell (1927) and Barraud and Covell (1928) have pictured the campaniform sensilla in their study on the cibaria of anopheline and culicine mosquitoes, but they grouped them with the dorsal papillae and trichoid sensilla, and called them dorsal papillae. Day (1954) is probably the first to recognize these sensilla as campaniform sensilla.

3.2.3. Dorsal Papillae

These are situated on the membranous dorsal wall of the cibarium, and only one pair is found in all the mosquitoes examined (Fig. 124).

In Anopheles, these papillae are located near the middle of the cibarium, and they are situated a short distance apart from each other (Fig. 125), as already noted by Sinton and Covell (1927). In A. albimanus, the two dorsal papillae are closely placed on the midline at the middle of the cibarium. Sinton and Covell (1927) erroneously identified both as one papilla. They also reported that A. argyritarsis female has only one dorsal papilla.

In Orthopodomyia, Barraud and Covell (1928) found that the dorsal papillae are located near the middle of the cibarium slightly apart from each other, as in Anopheles.

In all the cibaria of other mosquitoes listed in Appendix A, the dorsal papillae are situated one on either side of the posterior end of the dhp., immediately behind the campaniform sensilla (Figs. 126 - 135). Structurally, these papillae are similar to the palatal papillae in being socketed at the base, each having a thick, papillar shaft. In female Culiseta inornata, the tip of the papilla is slightly bifurcated (Fig. 145, arrow), and it is probably through there the papilla opens to the outside. From LM measurements, the diameter of the sockets ranges between 3 to 5 μ, and the length of the papilla is between 3 to 9 μ, with all Anopheles and most Culex mosquitoes examined having the shortest papillae, and longer ones are found in Toxorhynchites, Aedes and some Culex species.

3.2.4. Trichoid Sensilla

These are the "hair-like sensilla" of Day (1954) and von Gernet and Buerger (1966). They also are located on the anterior membranous dorsal wall of the cibarium, lateral to the campaniform sensilla (Fig. 124).

In Anopheles stephensi and A. merus, only one pair of trichoid sensilla are present (Fig. 125). Although Sinton and Covell (1927) did not mention in their text, their figures showed that in female Anopheles culicifacies, A. kochi, A. pulcherrimus, A. stephensi, and A. subpictus, the cibaria also have only one pair of trichoid sensilla. It is interesting to note here that these mosquitoes all belong to the subgenus Cellia. Trichoid sensilla are absent in female Malaya (=Harpagomyia) genurostris, and only one pair are present in male Anopheles culicifacies and Uranotaenia recondita (Barraud and Covell, 1928).

In Anopheles earlei, A. albimanus, and the rest of the mosquitoes listed in Appendix A where their cibaria were examined using LM, two to four trichoid sensilla are found on either side of the dhp. (Figs 126 - 135). In some cases, up to five of these can be found on one side (Fig. 127). The number of trichoid sensilla is either symmetrical on both sides of the dhp., or one side has one more sensillum than the other side. Barraud and Covell (1928) have also noted this difference, and suggested this was an artifact due to the displacement of the dorsal wall during dissection, so that one or more papillae may be hidden in a fold at the side. But this is not so, as in my study on Aedes aegypti, where I have examined the cibaria of 34 males and 32 females, such a difference is quite common, and the mosquitoes show sexual dimorphism in the total number of trichoid sensilla (Lee, 1974). Since the number of the specimens examined for each species in the present study was only two to five, it is not known whether such dimorphism exists in these species as well.

The trichoid sensillum is socketed at the base, and the seta gradually tapers to a fine point (Figs. 138, 144, 145). With LM measurements, the diameter of the socket ranges from 2 - 5 μ, and the seta 4 - 12 μ long, depending on the species. The longest setae are found in Anopheles, Toxorhynchites, and some Aedes mosquitoes, with Wyeomyia smithii, Psorophora and Culex species having seta only 4 - 7 μ long. In the rest of the mosquitoes studied here, the setae are 5.0 - 9.5 μ long.

Structurally, these sensilla resemble the trichoid sensilla described by Rice (1973) in the cibarial pump of the blowfly Calliphora erythrocephala. He found between 30 - 40 of these sensilla arranged

along the lateral sides of the median apodeme on the anterior (dorsal?) wall of the cibarium. The socket is 6 μ in diameter, and the seta 60 - 80 μ long. He also found that each sensillum is innervated at the base by a single dendrite. Rice et al. (1973a) also reported several trichoid sensilla in the cibarium of the tsetse fly. They found each seta is innervated at the base by a single dendrite. These setae are more slender than mosquito trichoid sensilla.

3.2.5. Ventral Papilla

These are found on the postero-ventral wall of the cibarium just cephalad of the opening of the cibarium into the pharyngeal pump (Fig. 124). Owen (1963) called them sensilla basiconica in his study on the females of Aedes dorsalis and Culiseta inornata. Sinton and Covell (1927) have noted the presence of these papillae in the female Anopheles mosquitoes they examined, and they called them ventral papillae. I here follow their terminology. Normally, four ventral papillae are found in the cibarium (Fig. 124).

In Anopheles mosquitoes, the ventral papillae are arranged in two ways. In A. farauti, A. stephensi and A. merus, the four papillae are arranged in a line or in a semicircle (Figs. 125, 146). But in A. earlei, they are arranged in a quadrangle at the middle of the postero-ventral surface of the cibarium, as in Culiseta and Culex mosquitoes (see below). In female A. farauti, an opening 0.15 μ in diameter is found at the tip of the papilla (Fig. 147). In A. albimanus, ventral papillae are seen in some preparations. But as already noted by Sinton and Covell (1927), the number of the ventral papillae is difficult to determine because of the thick cuticle around them. In most species, the socket diameter is

2.5 μ, and the papillae are mostly 2 μ long, except in A. earlei, where the papillae are 2.5 μ to 4.5 μ long.

It is uncertain if ventral papillae are present in Toxorhynchites rutilus, because the thick cuticle at the posterior end of the cibarium makes observation difficult. In male T. brevipalpis, only two ventral papillae are visible as one group on one side of the cibarium near the base of the lateral flange in any one specimen. In the females, all four ventral papillae are easily recognizable. They are arranged in groups of two each, each group situated at the base of the lateral flange, as in female T. splendens (Fig. 127). The socket of the ventral papilla is about 3 μ in diameter, and the papillae 2.5 - 5.0 μ long.

Only two ventral papillae are found in Wyeomyia smithii. They are located on the midline at the posterior edge of the cibarium (Fig. 126). The socket is 2.5 μ in diameter, and the papillae 4.5 μ in length.

In female Coquillettidia perturbans, the four ventral papillae are present as groups of two, and these groups are closely located to each other near the posterior end of the cibarium (Fig. 128). The socket is about 4 μ in diameter, and the papillae 3 μ long.

The ventral papillae in Psorophora species are arranged in two widely separated groups of two each (Fig. 130). The sockets are approximately 2 μ in diameter, and the papillae are 2.5 μ long in P. ferox and 2 - 5 μ long in P. varipes.

In Aedes mosquitoes, the four ventral papillae are situated in groups of two each, similar to the ventral papillae in C. perturbans (Figs. 129, 131, 148). The socket diameter ranges from 3.0 - 4.5 μ and the length of the papillae from 2.5 - 5.0 μ. In female A. aegypti,

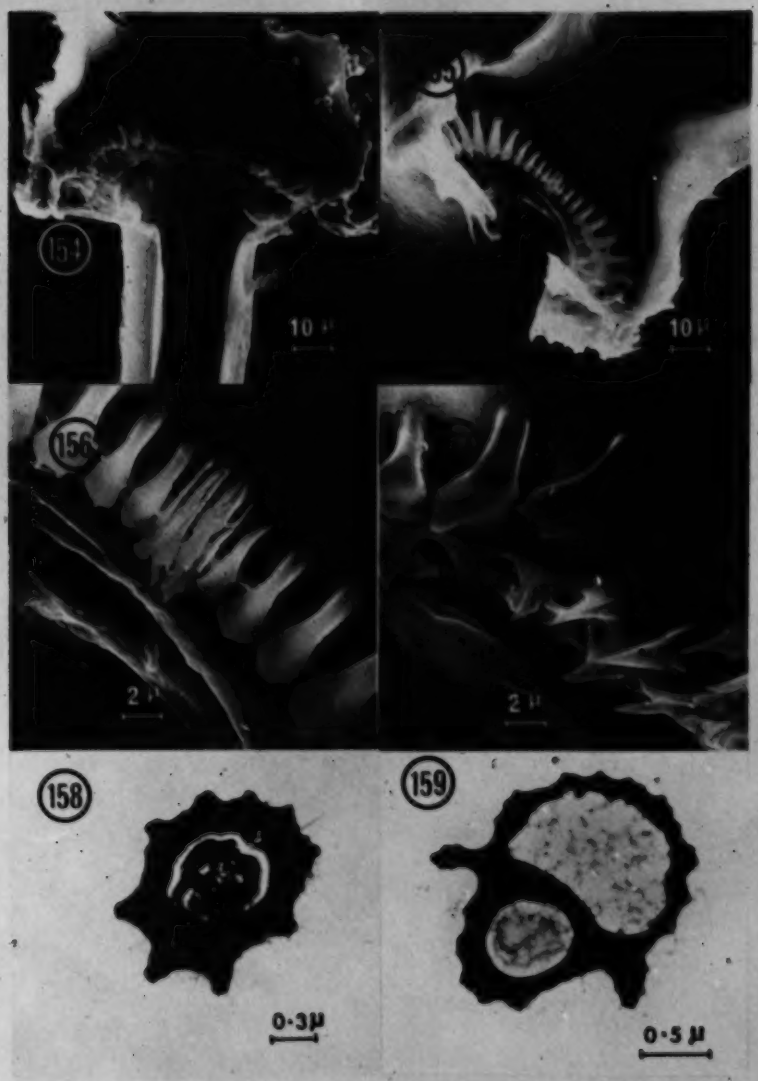
Figs. 148-153. Ventral papillae in the cibarium of female mosquitoes.
Fig. 148. Aedes aegypti. Note the quadrangular arrangement of the papillae.
Figs. 149 and 150. Higher magnification of the above, showing the apical opening of the papillae.
Fig. 151. Culiseta inornata. Note the absence of cibarial armature.
Figs. 152 and 153. Higher magnification of the above, showing the apical opening of the papillae. Note the papilla in Fig. 153 has a bifid tip.

the papillae are conical in shape, and each papilla has an opening about 0.15 μ in diameter at the tip (Figs. 149, 150).

Ventral papillae were found only in two out of the three male Armigeres subalbatus examined. In both cases, only two sockets each with a diameter of 3 μ were seen, but I could not find the papillar shafts. In the female of the same species, ventral papillae were absent in the six specimens studied. In Armigeres durhami, four ventral papillae arranged in a quadrangle are located on the mid-ventral posterior wall of the cibarium, though in some cases, two papillae on one side are very close together (Fig. 132). The sockets average 3 u in diameter, and the papillae averages 3.5 μ in length.

In Opifex fuscus, ventral papillae are found only in female mosquitoes. The four papillae are in groups of two, and the sockets are 3 μ in diameter (Fig. 133). The papillae are long and slender, measuring 10 - 12 μ in length, the longest in all the mosquitoes examined in this study.

In Culiseta and Culex, the four ventral papillae are arranged either in a line, or in a quadrangle, even in specimens of the same species, as in Culiseta inornata and Culex declarator (Figs. 151, 154, 155). The papillae in Culiseta inornata are slender in shape, and an opening approximately 0.2 μ in diameter is found at the tip of the papilla (Fig. 152). In some specimens, the tip of the papilla is bifid (Fig. 153). The shape of the papilla in Culex mosquitoes is conical (Fig. 154, 155), similar to Aedes aegypti. The socket diameter of the ventral papillae in Culiseta is 3.0- 4.5 μ, and the papillae 3 - 6 μ long. In Culex, the socket diameter is 2 - 4 μ, and the papillae are 2 - 3 μ long.



Figs. 154-157. Cibarial armature of female Culex declarator.
Figs. 154 and 155. Note the difference in the arrangement of the ventral papillae in the two specimens.
Figs. 156 and 157. Higher magnification of Fig. 155, showing the "teeth" at the midline (Fig. 156), and conical projections behind the "teeth" (Fig. 157).
Figs. 158 and 159. Transverse sections of the tarsal hair of female Aedes aegypti, showing one type of hair with one lumen, and the other type with two lumina.

Since the ventral papillae each have an opening at the tip, it is possible that these papillae function as thick-walled chemoreceptors. In the cibarium of the blowfly Calliphora erythrocephala, Rice (1973) found four basiconic sensilla arranged in a straight row on the posterior wall of the cibarium. He reported a circular opening less than 0.5 μ in diameter at the centre of each peg. But his SEM micrograph was too poor to show with any clarity whether there is really only one opening at the tip.

In the tsetse fly Glossina austeni, Rice et al, (1973b) found four basiconic pegs (LC4 receptors) arranged in a quadrangle on the dorsal edge of the posterior dorsal wall of the cibarium. They found that each sensillum is innervated by one bipolar neurone, with the dendrite extending to the tip through the central tube. At the tip of the peg, the centre is depressed, and the surrounding wall is castellated. In the blowfly and the tsetse fly, these basiconic sensilla are the only chemoreceptors in the cibarium.

3.3. Probable Function of the Cibarial Sense Organs

Using the vital methylene blue staining technique of Burgess and Rempel (1966), I found that the cibarial sense organs in female Aedes aegypti and female Culiseta inornata are innervated, but it was not possible to determine the number of dendrites associated with each sense organ. TEM study is needed to determine the exact number of dendrites associated with each type of cibarial sense organ. Dendrites from the dorsal wall sense organs of the cibarium are connected to a group of cells dorsal to the cibarium, as already reported by von Gernet and

Buerger (1966). They also noted that these cells are associated with fine neurones of labral nerve I, which is connected to the fronto-labral nerve, and the latter is joined to the frontal ganglion. Elevator muscles of the cibarium are also innervated by labral nerve I (von Gernet and Buerger, 1966). The ventral papillae are probably innervated by a small branch of the fronto-labral nerve (von Gernet and Buerger, 1966).

From the results of the SEM study, I found that the palatal, dorsal and ventral papillae resemble thick-walled chemoreceptors, and the trichoid and campaniform sensilla resemble mechanoreceptors. The probable function of these sense organs is discussed below, based on the behavioural observations of earlier workers. The discussion concerns female mosquitoes only, unless mentioned otherwise.

Mosquitoes show discontinuous suction when feeding on water and sugary solutions, and continuous suction when feeding on blood (MacGregor, 1930, 1931). Owen (1963) suggested that in sucking blood, the cibarial and pharyngeal pumps contract intermittently as the fascicular stylets penetrate the skin. Once a blood source is reached, contact with blood stimulates the cibarial sense organs to assume control of sucking until the mosquito is satiated. Schiemenz (1957) deduced a sequence of actions of the stylets and the pumps from his observations on feeding mosquitoes, in that the dilator muscles of the two pumps contract alternately. In any event, during feeding, when the liquid food reaches the cibarial pump, the palatal papillae may come into contact with the food first, thus detecting the nature of the food. Evidence from behavioural studies suggest that mosquito cibarial sense organs are sensitive to sugar and blood (Day, 1954; Hosoi, 1959; Owen, 1963, 1965) and also to unacceptable compounds (Owen, 1963; Salama, 1966). If the

food is acceptable, then the discontinuous pumping action of the pumps may change into continuous pumping until the mosquito is satiated (Owen, 1963).

If the food is unacceptable, the palatal papillae may also detect it as soon as it enters the cibarium. Mosquitoes are known to show signs of rejection to unacceptable compounds by stopping the aspiration (Owen, 1963; Salama, 1966). Owen (1963) was able to induce mosquitoes to feed on salt solutions, formaldehyde, and 95% ethyl alcohol, by stimulating the labella with 1M sucrose solution, and offering the above mentioned solutions separately through a capillary tube to the fascicle. Although intake ceases as soon as the solution reaches the cibarium, in some cases, repeated stimulation of the labella with sucrose will induce aspiration again. Some mosquitoes died while drinking the formaldehyde, and all were dead within one hour. This is because mosquitoes are unable to expel any unacceptable compounds present in the labral food canal and the cibarium (MacGregor, 1931). Any remnant of fluid along the labrum and the cibarium is always cleared by aspiration (Nuttall and Shipley, 1901; MacGregor, 1931). This last aspiration is important, especially when the mosquito is feeding on blood, as it prevents having blood coagulating in the food canal. Kadletz and Kusmina (1929) found that when blood sucking is interrupted, any fluid left in the labrum is diverted to the diverticula (from Christophers, 1960). In the blowfly Phormia regina, unacceptable compounds are normally regurgitated (Dethier, 1955).

The dorsal papillae are structurally very similar to the palatal papillae. It is possible these two groups of papillae serve a similar function in detecting the nature of food entering the cibarium. However,

Day (1954) suggested from his experiments that the dorsal papillae detect the particulate nature of the corpuscles in the blood.

The trichoid sensilla may be flow receptors, registering the flow of the food through the cibarium, a function already suggested for the trichoid sensilla in the cibarium of the tsetse fly Glossina austeni (Rice et al., 1973b) and the blowfly Calliphora erythrocephala (Rice, 1973).

The function of the cibarial campaniform sensilla is uncertain. Rice (1973) suggested that the campaniform sensilla in the blowfly cibarium are probably capable of detecting the viscosity of the fluid in the pump. But in mosquitoes, Hosoi (1954, 1959) found that viscosity of the fluid does not affect the feeding behaviour. Viscous fluids only protract the duration of aspiration.

In the cibarium of the tsetse fly Glossina austeni and the blowfly Calliphora erythrocephala, Rice (1970) found three multiterminal neurones on each side of the anterior wall which function to monitor the rate and type of cibarial pumping. Whether such neurones are also present in the mosquito cibarium is not known. The campaniform sensilla might function to monitor the pumping action of the cibarium. During the contraction of the cibarial elevator muscles, the cap-membrane of the campaniform sensilla will probably compress the tubular body above it longitudinally, which according to Chapman et al. (1973) is the most efficient stimulus for campaniform sensilla.

Between the oesophagus and the midgut, the mosquito has two small dorsal diverticula inserted between the flight muscles, and a large ventral diverticulum or crop with a long duct which lies in the abdomen. Behavioural studies have shown that blood meals enter the midgut and

sugary solutions are dispatched to the ventral diverticulum (Nuttall and Shipley, 1903; Wright, 1924; MacGregor and Lee, 1929; Kadletz and Kusmina, 1929; MacGregor 1930, 1931; Bishop and Gilchrist, 1946; Trembley, 1952; Day, 1954; Hosoi, 1954). Day (1954) and Hosoi (1954, 1959) have found independently that when a mixture of sugar and blood is given to a mosquito, the destination of the food is dependent on the relative concentration of the components. Thus a mixture with a higher concentration of blood will go to the midgut and that with a higher concentration of sugar will go to the ventral diverticulum. A mixture containing an equal proportion of the two will go partly to midgut and partly to the ventral diverticulum. Day (1954) suggested that the "pit organs" (campaniform sensilla?) in the cibarium may detect sugars, causing the relaxation of the sphincters of the ventral diverticulum, and the papillar sense organs (palatal papillae) detect the blood, causing the relaxation of the cardiac sphincter. Simultaneous stimulation of both groups of sense organs may result in relaxation of both series of sphincters. It is known that campaniform sensilla are mechanoreceptors (Pringle, 1938; Thurm, 1964; Chapman et al., 1973), and these obviously will not detect sugars. It is possible this mechanism is monitored through the ventral papillae, which are located near the junction between the cibarial and pharyngeal pumps. As soon as the food reaches the ventral papillae, the sphincter muscles of the crop or the midgut may relax depending on the nature of the food; blood enters the midgut, and sugary solutions go to the ventral diverticulum. Unacceptable compounds probably go to the diverticula, as do some poisonous fluids (MacGregor, 1930).

It appears the labellar hairs also play a role in the switching mechanism, as Hosoi (1959) reported in Culex pipiens pallens, that when a strong sugar stimulus is applied to the labella, sugar-free blood presented to the unsheathed fascicle passes not to the midgut, but to the ventral diverticulum.

That the ventral papillae might be involved in the switching mechanism of the food can probably be verified by studying the destination of the food in those mosquitoes where the ventral papillae are absent, (male Opifex fuscus, female Armigeres subablatus, and probably both sexes of Toxorhynchites rutilus). Of the species listed above, only Armigeres subalbatus is known to feed on blood, but nonblood-feeders might be induced to feed on blood as male mosquitoes have been induced to feed on blood in the laboratory (MacGregor, 1931; Russell, 1931; Day, 1954; Salama, 1966; Jones and Pilitt, 1973). Russell (1931) found in Culex quinquefasciatus, Aedes aegypti and Anopheles ludlowae and Day (1954) in Aedes aegypti that when male mosquitoes were induced to feed on blood, the blood went to the midgut. In most species, as the males have the same type of sense organs as the females, the function of these sense organs are probably similar in both sexes.

Such a switching mechanism in feeding behaviour occurs in other members of the Diptera also, and Megahed (1958) has extensively reviewed the studies regarding the destination of food in Diptera. In female Culicoides nubeculosus, Megahed (1958) found that blood always goes to the midgut. The oesophageal diverticulum serves as reservoir for water and sugar, but not for blood. In wild caught hematophagous females of the tabanid Chrysops vittatus, Lall (1970) found glucose and fructose in the diverticulum (crop). Wiesmann (1964) found that in Musca species

deprived of their labial chemoreceptors, the switching mechanism was still operative, where water and dilute solutions were sent to the midgut, and sugar and milk solutions went to the crop (cited from Rice, 1973).

3.4. Cibarial Armature

3.4.1. Structure and Taxonomic Implication

These are specialized structures present on the postero-ventral wall of the cibarium of the female Culex and some Anopheles mosquitoes (Figs. 125, 135), but are absent in the males of these genera, as already noted by Sinton and Covell (1927) and Michener (1944). In Anopheles, cibarial armature is found in the females of all species I studied except in A. earlei, which belongs to the subgenus Anopheles. As observed by Sinton and Covell (1927), members of the subgenera Anopheles and Bironella do not possess any cibarial armature.

The structure of the cibarial armature is quite elaborate, and differs from species to species. In A. stephensi, the cibarial armature consists of about 23 alternating long spines and short pegs (Fig. 125). In A. farauti, the cibarial armature is made up of six scale-like "teeth", with longitudinal striations that end in slender projections (Fig. 146). The base of each scale-like "tooth" is flanked on each side by two short cuticular projections (Fig. 146). These "teeth" are quite similar to the spines reported by Dapples and Lea (1974) in the ampulla of the hindgut of A. aegypti.

In female Wyeomyia smithii, and in both sexes of Opifex fuscus, horizontal rows of cuticular projections are found posterior to the posterior hard palate just anterior to the ventral papillae (Figs. 126,

133). But these are not homologous to the cibarial armature found in Anopheles mosquitoes. In Figure 5 of Dapples and Lea (1974), the posterior dorsal hard palate in the cibarium of A. aegypti is seen covered with fine, posteriorly directed spines, very similar to the ones in W. smithii and O. fuscus. They suggested that these spines probably act as a barrier between the cibarial and pharyngeal pumps.

The number of "teeth" in the cibarial armature varies from species to species. In Culex declarator, the cibarial armature consists of 22 - 23 spatulate "teeth" (Figs. 154 - 157). The median "teeth" in those specimens where the ventral papillae are arranged in a quadrangle are different from those where the ventral papillae are arranged in a semi-circle (Figs. 154 - 156). Two rows of conical cuticular projections are found posterior to the spatulate "teeth" (Fig. 157).

Sinton and Covell (1927) have examined the cibaria of 52 species of anopheline mosquitoes, and suggested the use of cibarial armature structure to differentiate species of anopheline mosquitoes. Barraud and Covell (1928) also pointed out the taxonomic importance of the cibarial armature in Anopheles and Culex mosquitoes. In these two genera, they noted that although similar cibarial armature may be found in two species, some species that were thought to be closely related differ strikingly in the structure of the armature.

Edwards (1941) figured the cibarial armature of five subgenera of Culex mosquitoes found in the Ethiopian Region, but did not use the armature as a diagnostic characteristic to separate the species.

Chwatt (1945) could find no difference between the cibarial armature of Anopheles gambiae and A. gambiae var. melas. The two subspecies

are normally differentiated by their breeding habits and the structure of the eggs.

Michener (1944) provided a key to separate some species of Culex found in the southeastern United States into groups, on the basis of female cibarial armatures. He noted that such a system can be used to separate members of the Culex (Melanoconion) complex. Females of the Melanoconion complex were generally considered inseparable (Knight and Haeger, 1971). Identification is based mainly on male genitalia. My preliminary study on four species of Culex mosquitoes belonging to this complex showed that the number of cibarial "teeth" in the cibarial armature can be very useful in separating closely related species. For instance, Culex ocossa and C. panocossa are so similar, that for years they were classified as one species, C. aikenii. It was only recently that Belkin (1970) separated them into two distinct species. The number of cibarial "teeth" is clearly quite different in these two species, in that C. ocossa has 31 - 32, and C. panocossa has 24 - 25 "teeth". The other two species studied here were C. erraticus, which has 7 - 8, and C. peccator, which has 39 - 44 cibarial "teeth"

Knight and Haeger (1971) suggested the use of the shape and colour of mesepimeron and mesepisternum, and also the type and arrangement of the scales on the thorax as diagnostic characteristics for females of the Melanoconion complex. As the scales are easily lost in light trap materials, the usefulness of the cibarial armature in separating species of such complexes should be investigated more thoroughly.

3.4.2. Function of the Cibarial Armature

Annett et al. (1901) suggested that the cibarial armature may assist in the valvular action of the cibarial pump, but they also pointed out that the armature may have a sensory function (cited from Sinton and Covell, 1927). However, the "teeth" in the cibarial armature do not resemble any sensory structure, and it is unlikely that they are sensory in function.

Patton and Evans (1929) noted that the armature, together with the membranous area at the junction between the cibarium and the pharyngeal pump, may form a valve which they called the "pharyngeal valve". The cibario-pharyngeal valve is elevated by a pair of valvular muscles from the frons (Thompson, 1905). But since the majority of mosquitoes are without the cibarial armature and they do not show any significant difference in their feeding behaviour from those with the armature, the valvular function of the armature is not plausible and the function of the cibarial armature still awaits further investigation.

Recently, Bryan et al. (1974) reported that the cibarial armature in mosquitoes damages the microfilariae of Brugia pahangi, causing loss of mobility and cuticular abrasions to the parasites as they found the proportion of damaged, non-motile microfilariae was higher in Anopheles species than in Aedes mosquitoes (cibarial armature being absent in Aedes species).

4. Tarsal Hairs

A preliminary study of the tarsal hairs in female Aedes aegypti showed that two types of hair are present: one with a single lumen, and the other with a double lumina (Figs. 158 and 159), similar to the aboral labellar hairs. Slifer (1961) using crystal violet staining has described the distribution of tarsal hairs with stainable tips in both sexes of A. aegypti. She suggested that hairs with stainable tip are gustatory receptors. Owen (1963) reported in female Culiseta inornata that the tarsal chemosensory hairs are double-chambered. Behavioural studies have suggested that mosquito tarsal hairs are sensitive to water and sugar solutions (Frings and Hamrum, 1950; Feir et al., 1961; Owen, 1963, 1967, 1971), and are important in selecting oviposition sites (Wallis, 1954). Since the tarsal hairs are the first sense organs to come into contact with the host skin after the mosquito has landed, these double-chambered hairs might play an important role in the discrimination of the host.

IV. GENERAL DISCUSSION AND CONCLUSIONS

From behavioural studies, mosquitoes are known to be attracted by host odors, CO_2, warmth, humidity, and optical stimuli. Hocking (1971) has extensively reviewed the blood-sucking behaviour of mosquitoes and other terrestrial arthropods. In nature, mosquitoes also feed on plant nectar, and such feeding affects the longevity and dispersal potential of mosquitoes (van Handel, 1972). In the following discussion, the probable chain of events regarding the feeding behaviour of mosquitoes after landing on a host is suggested based on the results from this study and the reports of other workers.

Mosquitoes often walk around soon after landing on a suitable host and probably detect the acceptability of the host using the chemoreceptors located on the tarsi of the pro- and mesothoracic legs. Tarsi of the metathoracic legs may not be important in host discrimination, as the hind legs are often raised off the substrate when the mosquito is walking around. Behavioural studies have suggested that mosquito tarsal hairs are sensitive to sugar, salt and water (Frings and Hamrum, 1950; Owen and Larsen, 1963; Owen, 1971). Frings and Hamrum (1950) found in Aedes aegypti that stimulation of the tarsal hairs with NH_4Cl only made them restless, but the mosquito did not look for a more suitable substrate. Jones and Pilitt (1973) found that when all the tarsi of female A. aegypti were removed, the mosquitoes were still able to pierce the skin and take a blood meal rapidly, indicating that the tarsi are not essential in providing the force for

piercing. The number of dendrites associated with the tarsal hairs remains to be studied.

Probing of the substrate using the two labellar lobes follows shortly after landing. The long labellar hairs probably monitor the positioning of the labellar lobes, with the medium-sized hairs near the labellar tip and the apical hairs detecting the suitability of the host. The medium-sized hairs posterior to the tip of the lobes probably detect the odour(s) from the host.

When feeding on plant nectar, the presence of sugars may be detected by the labellar chemosensory hairs, so that the two lobes then spread apart, thus bringing the labral food canal opening to the solution. The chordotonal organs in the labellar lobes may monitor the spreading and closing together of the lobes. The spreading of the labella also brings the ligula into contact with nectar, and this contact causes the ligula to increase in size. The function of this swelling of the ligula may be two fold. One is to spread the solution over the ligular surface, thus bringing the solution into contact with the oral papillae, thereby mediating the sucking of the solution, as suggested by Larsen and Owen (1971). The other is probably to hold the labral tip in place, and serve as a mechanical support, since the tip of the fascicle is situated in the dorsal groove of the ligula. During nectar feeding, the mosquito shows discontinuous suction (MacGregor, 1930, 1931). The food passing over the labral campaniform sensilla may affect the pumping action of both cibarial and pharyngeal pumps. The above description applies to both sexes of mosquitoes.

When feeding on blood, secretion present on the host skin, and also host odour probably stimulate the labellar chemosensory hairs. Now the labellar lobes do not spread apart, but are held tightly together. The penetration of the fascicle into the host tissue is aided by the alternating cutting action of the laciniae (Robninson, 1939). The overlapping mandibles probably cover the opening of the labrum during penetration, to prevent the tissue from entering the food canal. Similarly, interdigitating finger-like projections at the tip of the hypopharynx may prevent possible blockage of the apical salivary canal opening by the tissue.

During the initial insertion, the substance blocking the opening of the labral sense organs may get rubbed off by friction with the tissue, thus exposing the receptor sites.

The fascicle is very flexible in the host tissue, as it often bends dorsally at almost a right angle to the plane of insertion after entering the skin, and the tip of the fascicle is capable of bending in different directions (Gordon and Lumsden, 1939; Griffiths and Gordon, 1952). Muscles controlling the two walls of the labrum are responsible for the dorsal and ventral flexion of the fascicle, and the differential actions of the laciniae are responsible for lateral flexion (Waldbauer, 1962). The apical and subapical sensilla probably detect the presence of blood (Salama, 1966; Lee, 1974) and the stimulating factor in the blood is probably the adenine nucleotides (Hosoi, 1959; Galun et al., 1963; Galun and Rice, 1971). Owen and Reinholz (1968) found in Culiseta inornata that water satiated mosquitoes refused 5-adenylic acid, ADP and ATP in Tris Buffer, whereas thirsty

mosquitoes imbibed these solutions. They therefore suggested that the acceptance of nucleotides was mediated by the water receptor.

As soon as a blood source is detected, the retractor muscles of the mandibles contract, exposing the opening of the food canal. Entry of food into the labral food canal may be detected by the labral campaniform sensilla, which may influence the action of the cibarial and pharyngeal pumps.

The mosquito may feed by inserting the fascicle into a capillary (capillary feeding), or feed from the hemorrhage in the tissue caused by the puncture (pool feeding), with the average time for capillary feeding 3 minutes and 10 minutes for pool feeding (Gordon and Lumsden, 1939; Griffiths and Gordon, 1952). Capillary feeding is more frequent than pool feeding (O'Rourke, 1956). Saliva is injected at different stages of penetration as tiny "puffs" (Gordon and Lumsden, 1939), and such injection probably continues even after a blood supply is tapped (Griffiths and Gordon, 1952).

Palatal and dorsal papillae probably monitor the chemical nature of the food. Indeed mosquitoes stop aspiration as soon as unacceptable compounds enter the cibarium (Owen, 1963; Salama, 1966). If the food is blood, then the discontinuous suction is changed into continuous suction until the mosquito is satiated (Owen, 1963). The trichoid sensilla probably register the flow of the food into the pump and the cibarial campaniform sensilla may monitor the pumping action of the cibarium. The ventral papillae probably detect the type of food thus providing the information for the initiation of the switching mechanism: sugar solutions enter the ventral diverticulum and blood goes to the

midgut. The two small dorsal diverticula probably function as air-separators, trapping air that comes in with the food (MacGregor, 1930; Day, 1954). Sugar solution stored in the ventral diverticulum is gradually passed to the midgut for absorption (MacGregor, 1931). Gooding (1972) has briefly reviewed the significance of storing sugar solutions in the diverticulum. Day (1954) suggested that as a blood meal is required by a majority of female mosquitoes to mature their eggs, the ability to take a blood meal in spite of a recent nectar meal is of survival value. Another theory is that sugar solution in the diverticulum serves as a supply of water.

Termination of feeding is initiated by the intersegmental abdominal stretch receptors (Gwardz, 1969). Withdrawal of the fascicle from the host tissue is aided by the laciniae, and Robinson (1939) and Jones and Pilitt (1973) have given detailed descriptions of this. In W. Horsfall's film on female Aedes aegypti feeding on frog foot-web, injection of saliva is seen also during the withdrawal of the fascicle. The labellar lobes probably help the fascicle to return into the labial gutter after withdrawal (Robinson, 1939).

The present study includes only some of the sense organs that are involved in the feeding behaviour of the mosquitoes and electrophysiological studies are needed to gain a better understanding of the function of these sense organs.

It is a well known fact that some people are not attractive to mosquitoes. Skinner et al. (1965) have reported the repellency of skin-surface lipids obtained from the foreheads or arms of humans to female Aedes aegypti, but the repellent still remains to be identified. But

as already suggested by Dethier (1973) for lepidopterous larvae, ingestion depends not on the presence or absence of a single stimulant or deterrent, but on the total impression derived from an integrated response to multiple components. A detailed knowledge of the receptors involved in the feeding behaviour of mosquitoes is necessary for a systematic approach to the development of effective repellents against these insects.

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Appendix A

A list of species used in this study and their source. Species where their labrum (lbr), mandibles (md), hypopharynx (hypx) and cibarium (cib) were studied using SEM are marked with a + under their respective column. ++ = studied with LM only; +++ = both LM and SEM were used. Under the labrum and cibarium, species where only one sex was studied are also indicated.

Species	Material Source	lbr	md	hypx	cib
Anopheles (*Anopheles*) *earlei* Vargas, 1943	JH	+			++
Anopheles (*Nyssorhynchus*) *albimanus* Wiedmann, 1820	USDA-L, TBN	+		+	++
Anopheles (*Cellia*) *farauti* Laveran, 1902*	LSHTM	+	+		+
Anopheles (*Cellia*) *stephensi* Liston, 1901	TBN	+	+	+	++
Anopheles (*Cellia*) *merus* Dönitz, 1902	LSHTM	+		+	++
Toxorhynchites (*Lynchiella*) *rutilus* (Coquillett), 1896	USDA-L, WU	+		+	++
Toxorhynchites (*Toxorhynchites*) *brevipalpis* Theobald, 1901	ND,WU	+			++
Toxorhynchites (*Toxorhynchites*) *splendens* (Wiedemann), 1819	G & B	++			+++♀
Trichoprosopon digitatum (Rondani), 1848	UWI-T	+		+	
Wyeomyia smithii (Coquillett), 1901	UM	+			++

* The species studied here is *A. farauti* No. 2 of Bryan and Coluzzi (1971)

Species	Material Source	lbr	md	hypx	cib
Coquillettidia pertubrans (Walker), 1856	JH	+♀♀		+	++♀♀
Uranotaenia lowii Theobald, 1901	USDA-L	+		+	
Orthopodomyia signifera (Coquillett), 1896	USDA-L	+			
Psorophora (Janthinosoma) ferox (Humboldt), 1819	USDA-L	+		+	++
Psorophora (Janthinosoma) varipes (Coquillett), 1904	USDA-L	+		+	++
Eretmapodites chrysogaster, Graham, 1909	YU	+			
Aedes (Ochlerotatus) canadensis (Theobald), 1901	JH	+			++♀♀
Aedes (Ochlerotatus) communis (De Geer), 1776	Lee	+♀♀		+	++♀♀
Aedes (Ochlerotatus) dorsalis (Meigen), 1830	JH, BR	+		+	++♀♀
Aedes (Ochlerotatus) excrucians (Walker), 1856	Lee	+			
Aedes (Ochlerotatus) fitchii (Felt & Young), 1904	JH, Lee	+			++♀♀
Aedes (Ochlerotatus) flavescens (Muller), 1764	JH, Lee	+	+	+	++♂♂
Aedes (Ochlerotatus) pionips (Dyar), 1919	Lee	+♀♀	+	+	
Aedes (Ochlerotatus) spencerii (Theobald), 1901	JH, BR	+			++♀♀
Aedes (Ochlerotatus) trichurus Dyar , 1904	G & B				++♀♀
Aedes (Finlaya) atropalpus (Coquillett), 1902	UM	+♀♀		+	++♀♀
Aedes (Finlaya) togoi (Theobald), 1907	TBN, IMR	+	+	+	++♂♂
Aedes (Stegomyia) aegypti, (L.), 1762	Lee, IMR				+♀♀

Species	Material Source	lbr	md	hypx	cib
Aedes (Stegomyia) polynesiensis Marks, 1951	ND	+		+	++
Aedes (Aedimorphus) vexans (Meigen), 1830	BR, JH, Lee	+	+	+	++
Aedes (Aedes) cinereus Meigen, 1818	JH	++♀	+	+	
Armigeres (Armigeres) durhami Edwards, 1917	IMR	+	+	+	++
Armigeres (Armigeres) subalbatus (Coquillett), 1898	IMR, ND	+		+	++
Opifex fuscus (Hutton), 1902	DAC	+		+	++
Culiseta (Culiseta) alaskaensis (Ludlow), 1906	JH, BR	+		+	++♀
Culiseta (Culiseta) inornata (Williston), 1893	JH, BR	+	+	+	+++
Culiseta (Culicella) morsitans (Coquillett), 1902	JH	+			++
Culiseta (Climacura) melanura (Coquillett), 1902	YU	+			
Culex (Lutzia) fuscanus Wiedemann, 1820	G & B				++
Culex (Neoculex) territans Walker, 1856	USDA-L, JH	+		+	
Culex (Culex) declarator Dyar & Knab, 1906	UWI-T	++♀	+		+
Culex (Culex) pipiens fatigans Wiedemann, 1828	TBN, ND, YU	++			++♀
Culex (Culex) pipiens molestus Forskal, 1775	TBN	+		+	
Culex (Culex) pipiens pipiens L., 1758	USDA-L	++			++
Culex (Culex) pipiens quinquefasciatus Say, 1823	USDA-L, GML	++			
Culex (Culex) salinarius Coquillett, 1904	USDA-L, YU	++			++

Species	Material Source	lbr	md	hypx	cib
Culex (Culex) tritaeniorhynchus Giles, 1901	TBN	+		+	
Culex (Culex) tarsalis Coquillett, 1896	G & B				++
Culex (Melanoconion) erraticus (Dyar & Knab), 1906	GML	++			++
Culex (Melanoconion) ocossa Dyar & Knab, 1919	GML	++			++
Culex (Melanoconion) panocossa Dyar, 1923	GML	++			++
Culex (Melanononion) peccator Dyar & Knab, 1909	USDA-L	++			++
Deinocerites pseudes Dyar & Knab, 1909	GML	+++♀			

Appendix B

List of Abbreviations used for Material Source

BR	Brian Rolseth, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada. (Collections from around Edmonton area).
DAC	Dr. D. A. Craig, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada. (Collected from Taylor's Mistake, Banks Penn., New Zealand).
G & B	G. von Gernet and G. Buerger, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada. (Mosquito mouthpart whole mounts they made for their 1966 study).
GML	Dr. David C. Baerg, Gorgas Memorial Laboratory, P. O. Box 2016, Balboa Heights, Canal Zone. (From lab colonies).
IMR	The Director, Institute for Medical Research, Kuala Lumpur, Malaya. (From lab colony).
JH	James Hudson, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada. (Mostly field collections from George Lake and Edmonton, Alberta).
Lee	My own collections around Edmonton area
LSHTM	Dr. Joan H. Bryan, London School of Hygiene and Tropical Medicine, Keppel Street (Gower Street), London WCIE 7HT. U.K. (From lab colonies).

ND — Dr. George B. Craig, Jr.,
Department of Biology,
University of Notre Dame,
Notre Dame, Indiana 46556,
U.S.A. (From lab colonies).

TBN — Professor F. Kuhlow, Ph.D.,
Department of Entomology,
Tropeninstitut,
Bernhard-Nocht-Strasse 74,
2 Hamburg 4,
Germany. (From lab colonies).

UM — Dr. R. Brust,
Department of Entomology,
University of Manitoba
Winnipeg, Manitoba,
Canada. (From lab colonies).

USDA-L — Dr. H. C. Chapman,
USDA Agricultural Research Service,
Gulf Coast Mosquito Research Laboratory,
803 Avenue J - Channault,
Lake Charles, Louisiana 70601
U.S.A. (Mostly from lab colonies).

UW — Dr. Stephen M. Smith,
Department of Biology,
University of Waterloo,
Waterloo, Ontario,
Canada. (From lab colonies).

UWI-T — John B. Davies
Trinidad Regional Virus Laboratory,
University of West Indies
P. O. Box 164, Port-of-Spain, Trinidad,
West Indies. (From lab colonies).

YU — Dr. Robert C. Wallis,
Department of Epidemiology and Public Health,
Yale University, School of Medicine,
60 College Street,
New Haven, Connecticut 06510
U.S.A. (From lab colonies).